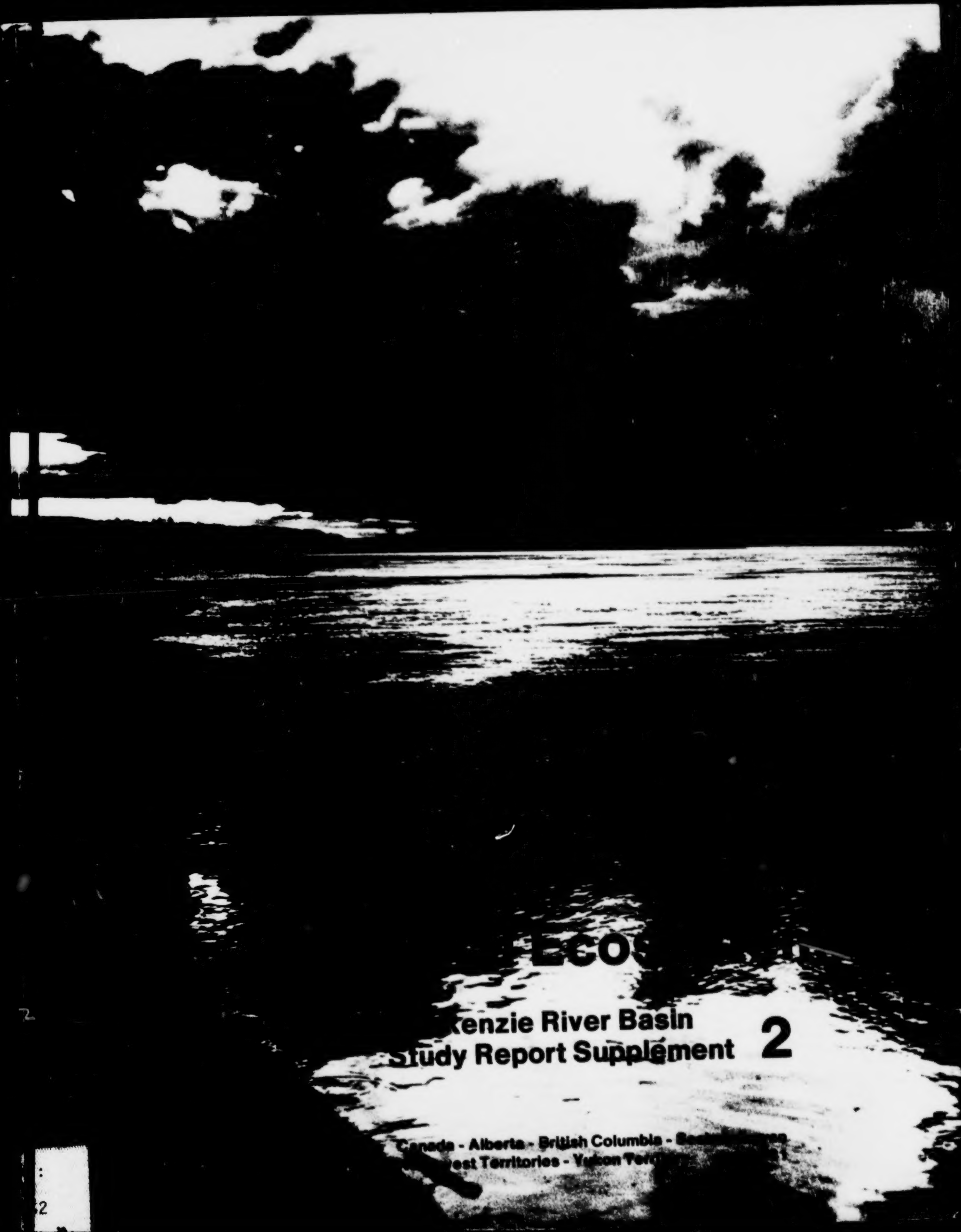

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Study Report Supplement 2

Canada - Alberta - British Columbia -
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List of Supplements

1. Sensitive Areas: Literature Review. WATDOC References
2. Alluvial Ecosystems
3. Spring Breakup
4. Hydrometeorologic Network Design
5. Hydrometeorologic Network Design: Background Reports
6. Slave River Delta
7. Athabasca Sand Dunes in Saskatchewan
8. Daily Hydrologic Model User Manual
9. Water Quality

This report was prepared for the Mackenzie River Basin Committee. Any conclusions, recommendations or opinions expressed herein are those of the authors and are not necessarily the same as those of the Committee.

Cover Photo: Mackenzie River at
Fort Simpson, Northwest
Territories, looking downstream

Mackenzie River Basin Committee

Alluvial Ecosystems

Mackenzie River Basin Study Report Supplement 2

A report under the 1978-81 Federal-Provincial Study Agreement respecting the water and related resources of the Mackenzie River Basin.

Canada - Alberta - British Columbia - Saskatchewan
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EXECUTIVE SUMMARY

The terms of reference for the study called for three specific steps:

- assembly of existing biophysical information from the Mackenzie River Basin, as well as from other major northward-flowing rivers in the circumpolar region, and evaluation of this information for relevance to the study;
- synthesis of information on relationships between physical and biological components of northern alluvial habitats, with particular attention to alluvial sites in the Mackenzie River Basin;
- analysis and description of ecological processes involved in the natural creation, maintenance and loss of plant communities and wildlife habitats in the Mackenzie River Basin.

The area of geographic coverage for this study included all of the Mackenzie River Basin. Within individual valleys, the area of interest extended laterally to the upper limit of alluvial deposits, including ancient terraces that are now well above the level of the most extreme recorded floods. Non-alluvial upland sites were discussed where this was necessary to account for wildlife life cycle or habitat relationships and where deliberate comparisons were made between alluvial and non-alluvial sites.

The Mackenzie River Basin drains one-fifth of the total area of Canada and its area of almost 2 000 000 km^2 makes it one of the world's largest river systems. In a Canadian context, the Mackenzie River system has both the largest drainage area and greatest river length, flowing approximately 4 000 km from the Finlay River headwaters in British Columbia to the Beaufort Sea.

Spring break-up and the snowmelt flood are the major hydrological events each year in rivers of the Mackenzie River Basin. Physical and biological processes that are tied to these annual events have a direct bearing on the productivity of alluvial landforms along rivers and streams in the basin. In turn, biological productivity of alluvial sites determines the rate at which renewable resources are produced along rivers in the basin. Waterways of the basin are the focus for a wide range of human uses that collectively exceed the variety of land uses possible further away from the river. Thus, the web of events that are tied to the spring break-up have a pervasive relationship to a wide variety of human uses of rivers and their adjacent alluvial ecosystems.

Flooding and subsequent reductions of water levels appear to be the key external forces that determine vegetational composition and productivity on floodplains. Evidence from a broad range of ecological studies indicates that with animal populations, both density and diversity of species tends to be higher at the land-water ecotone than in adjacent uplands.

Superimposed upon the distinctive ecological processes within alluvial sites are certain specialized features of resident species. Some animals that inhabit alluvial ecosystems are particularly well adapted either to take advantage of opportunities offered by a rapidly changing environment or to avoid some negative consequences of it. Waterfowl are among the flexible species. Birds that would normally nest on the prairies can bypass them in years of drought and spend the summer on northern deltas. Other examples of wildlife adaptations centre around reproductive potential once favourable conditions are created by flooding and

by low water levels. For instance, muskrats are prolific and can colonize newly created habitats soon after they become available.

The major deltas of the Mackenzie River Basin - the Peace-Athabasca, Slave, and Mackenzie - are among the largest concentrations of wetlands in the basin. Their areal extent and their many lakes, in contrast to the essentially linear nature of river valley alluvial areas, provide habitats for vegetation and wildlife unlike those along the rivers.

Although alluvial sites make up a small percentage of the total area within the Mackenzie River Basin, studies of forest and agricultural potential within the basin have confirmed findings from elsewhere that alluvial sites are among the most productive sites in any given region.

The distinct plant and animal communities of alluvial sites, and their relatively high productivities, are the end result of a complex web of climatic, fluvial and biological processes that interact to form areas of special significance along river channels and on deltas of the Mackenzie River Basin. The processes involved in these intricate relationships are a result of depositional and erosional forces, vegetational responses to fluvial processes, vegetational controls over wildlife use of alluvial sites, and a variety of ecological and physiological adaptations that allow resident plant and animal species to effectively use the dynamic habitats of flood-prone areas.

Added to the special features of alluvial sites, outlined above, is the fact that non-deltaic alluvial sites are located in river valleys that possess additional features of special importance to plant and animal communities. The physiographic diversity and distinctive microclimates of valley slopes give river valleys other features of biological importance, in addition to the special characteristics that typify flood-prone parts of the valleys.

Information that is currently available tends to focus on processes associated with long-term trends such as ecological succession and with events that follow catastrophic or spectacular events such as high floodwaters. However, some of the less dramatic events that occur each year, such as gradual lowering of water levels, are not well documented yet in relation to the life cycles and vitality of plants and animals that inhabit areas subject to annual fluctuations of water levels.

Although studies to date have provided considerable ecological information on specific sites and processes in both alluvial and non-alluvial areas of the Mackenzie River Basin, there is still a surprising lack of information. Many of the studies that have been done refer to locations which the reader cannot identify as alluvial or non-alluvial. When one wishes to make specific comparisons between alluvial and non-alluvial sites, there are no standardized measurements that could yield comparative data in terms of biological productivity, nutrient content of vegetation eaten by wildlife and relative uses of alluvial and non-alluvial areas for animals that seasonally move from one to the other. If such data could be obtained, they could be integrated with the many things that are already known about hydrologic processes in the Mackenzie River Basin. With such an integration, it would be possible to better understand the relative overall importance of alluvial sites for man and other species that live on or near alluvial areas.

WESTERN ECOLOGICAL SERVICES (BRITISH COLUMBIA) LTD.

10 June 1981

Mr. Hans Foerstel
Mackenzie River Basin Task Force,
Inland Waters Directorate
1901 Victoria Ave.,
Regina, Saskatchewan,
S4P 3R4

Dear Mr. Foerstel:

We are pleased to submit a report entitled **ALLUVIAL ECOSYSTEMS OF THE MACKENZIE RIVER BASIN** by E.B. Peterson, L.M. Allison and R.D. Kabzems. The report is a result of a contract issued by the Inland Waters Directorate under the auspices of the Mackenzie River Basin Study Program (D.S.S. Contract No. KL364-9-0242, Serial No. OSS79-00194). The review of ecological information in this report was prepared jointly by Western Ecological Services (B.C.) Ltd., Sidney, British Columbia, and Salix Enterprises Ltd., Cowley, Alberta.

In addition to the written report, this project resulted in selection of approximately 130 color slides from the Dr. Don Gill Memorial Slide Collection, Department of Geography, University of Alberta; the selected slides have been indexed to specific sections of the attached report and will be reproduced by the Inland Waters Directorate, Regina, for possible audio-visual portrayal of ecological processes in alluvial sites of the Mackenzie River Basin.

For technical assistance during preparation of this report we thank the following: Randy Packan and Peter Kershaw, Department of Geography, University of Alberta for assistance with selection of slides from the Dr. Don Gill Memorial Slide Collection; Don Blood (Donald A. Blood and Associates, Lantzville, B.C.), Rolf Kellerhals (Kellerhals Engineering Services Ltd., Heriot Bay, B.C.), and Steve Zoltai (Northern Forest Research Centre, Edmonton, Alta.) for technical review of an earlier

... 2

draft of the report; Merle Peterson for library searching; Bruce Peterson for preparation of maps and drawings; and Glenda Mersky and Michelle Peterson for manuscript preparation.

We hope that you find the report a helpful background document for the Mackenzie River Basin Study Program.

Yours sincerely,

WESTERN ECOLOGICAL SERVICES (B.C.) LTD.
PER:

Everett B. Peterson
President

CONTENTS

PAGE

Executive Summary i

Letter of Transmittal iii

Contents v

List of Tables ix

List of Figures x

I. INTRODUCTION 1

A. Study Objectives 1

B. The Mackenzie River Basin 3

C. Spring Break-up and Other Special Features of Northern Rivers 3

D. Major Deltas in the Mackenzie River Basin 8

E. Flood-prone Areas as Biophysical Systems 10

II. HYDROLOGIC FEATURES RELATED TO GEOMORPHIC AND VEGETATIONAL PROCESSES 15

A. Hydrologic Processes Important for Alluvial Vegetation and Wildlife During Floods 15

1. Flooding During Spring Break-up 15

a. Spring break-up in the Mackenzie River Basin . 15

b. Areas subject to most severe flooding in spring 16

2. Ice-Floodwater Interactions 17

a. Ice jams in the Mackenzie River Basin 17

b. Ice-shove zones 18

c. Ice effects upon vegetation during flood periods 18

CONTENTS (Cont'd.)

PAGE

3. Summer Floods 19
   a. Summer floods in delta areas 19
   b. Summer floods in non-deltaic areas 20

B. Hydrologic Processes Important for Alluvial Vegetation and Wildlife during Non-flood Periods ... 22
   1. Fluctuations of water levels 22
   2. Reversals of flow in delta channels 23
   3. Complete freezing of water bodies 23
   4. Delta hydrology under regulated flow 24

III. CLIMATIC CONDITIONS DURING FLOOD PERIODS 25
   A. Climate in Relation to Spring Break-up 25
   B. Climate in Relation to Summer Storms 26
   C. Permafrost Interactions with Fluvial Processes 28

IV. THE LIFE AND DEATH OF ALLUVIAL LANDFORMS 33
   A. Channel Systems 33
   B. Sediments 34
   C. The Battle Between Depositional and Erosional Processes 36
   D. Islands and Channel Bars 37
   E. Levees and Floodplains 38
   F. Deltas and Delta Lakes 39

V. VEGETATION IN ALLUVIAL AREAS 43
   A. Plant Succession on Deltaic Alluvial Sites 44
   B. Plant Succession on Non-deltaic Alluvial Sites 48
   C. Productivity of Vegetation on Alluvial Sites 57

CONTENTS (Cont'd.)

PAGE

VI. WILDLIFE AND WILDLIFE HABITAT IN ALLUVIAL AREAS 62

A. Wildlife and Wildlife Habitat of Major Delta Areas 62

1. Birds 62

a. Peace-Athabasca Delta 62

b. Slave Delta 67

c. Mackenzie Delta 69

2. Aquatic Furbearers 71

a. Peace-Athabasca Delta 72

b. Slave Delta 73

c. Mackenzie Delta 73

3. Ungulates 76

a. Peace-Athabasca Delta 76

b. Mackenzie Delta 77

4. Marine Mammals 77

B. Wildlife and Wildlife Habitat of Non-deltaic Alluvial Areas 78

1. Birds 78

2. Aquatic Furbearers 80

3. Terrestrial Furbearers 80

4. Ungulates 81

C. Comparisons of Wildlife Species and Habitats on Alluvial and Non-alluvial Areas 84

D. Nutrients available to Wildlife in Alluvial Ecosystems . 85

CONTENTS (Cont'd.)

PAGE

VII. ECOLOGICAL PROCESSES IN ALLUVIAL ECOSYSTEMS: A SYNTHESIS 88

A. Fluvial Processes that Build Alluvial Habitats 89

B. Fluvial Processes that Destroy Alluvial Habitats 91

C. Annual Fluvial Processes that Influence Alluvial Vegetation and Wildlife 92

D. Vegetational Influences upon Physical Processes in Alluvial Habitats 95

E. Long-Term Successional Processes in Alluvial Habitats .. 97

F. Adaptations of Plants and Animals for Opportunistic Use of Alluvial Habitats 99

G. Conclusions 101

REFERENCES 104

APPENDIX 1 GLOSSARY OF TECHNICAL TERMS 120

APPENDIX 2 COMMON AND SCIENTIFIC NAMES OF PLANTS REFERRED TO IN TEXT 124

APPENDIX 3 COMMON AND SCIENTIFIC NAMES OF MAMMALS REFERRED TO IN TEXT 127

APPENDIX 4 COMMON AND SCIENTIFIC NAMES OF BIRDS REFERRED TO IN TEXT 128

LIST OF TABLES

TABLE		PAGE
1	Forest productivity, in terms of average mean annual increments (m^3/ha/yr), for balsam poplar, white spruce, black spruce and white birch in vegetation units of the Mackenzie River valley	60
2	An estimation of the relationship of waterfowl densities and numbers to various water-level regimes in the Peace-Athabasca Delta, 1971-76	65
3	Bison seasonal distribution and habitat use in Wood Buffalo National Park	77

LIST OF FIGURES

FIGURE		PAGE
1	The Mackenzie River Basin	2
2	Mean annual flow of Mackenzie River and its main tributaries	4
3	River and settlement place names used in the text, Mackenzie River Basin	5
4	Spring break-up on the Mackenzie River	6
5	Peace-Athabasca Delta geographic features and place names	9
6	Slave Delta geographic features and place names	11
7	Mackenzie Delta geographic features and place names	12
8	Boulder pavement in ice-shove zone at channel margin	17
9	Driftwood, boulder pavement, and an ice-pushed ridge on bank of Liard River, 18 km south of Fort Simpson	18
10	Ice-scarred poplar tree as an indicator of maximum ice shove levels, Mackenzie River opposite Green Island	18
11	Alluvial vegetation mat crumpled by summer floodwaters along tributary of Mountain River, N.W.T.	21
12	Adventitious roots on stem of white spruce that was successively surrounded by alluvial sediments during floods	23
13	"Reverse" delta built into lake on Mackenzie Delta	24
14	Flooding of snow and ice surface by floodwaters in spring	27
15	Distribution of permafrost and unfrozen ground along an actively shifting channel in the Mackenzie Delta	29
16	Undercut river bank in Mackenzie Delta	30
17	Snow accumulation in willow zone of point bar environment of Mackenzie Delta	32

LIST OF FIGURES (Cont'd)

FIGURE PAGE

18 Adventitious root development in three-year-old white spruce seedling after alluvium was deposited over decayed wood on which the seedling had originally germinated, Slave River Lowlands 36

19 Variation in form of tree bases in relation to rate of deposition 36

20 Initiation of plant succession on new ground formed by deposition of sediments during floods 37

21 Point bar formation in a laterally migrating channel .. 38

22 Semi-active part of a delta with a log-filled cut-off channel that is active only during high floods 40

23 Thermokarst lake in Mackenzie Delta 41

24 Mature white spruce on upper levee along channel in Mackenzie Delta 45

25 Successional associations and environmental conditions along a point bar traverse in the Mackenzie Delta 49

26 Changes in sedimentation, forest cover, understory species richness, tree density, moss cover, and frozen ground in relation to channel migration on the Beatton River floodplain in northeastern British Columbia 50

27 Balsam poplar on point bar in Mackenzie Delta 51

28 Typical vegetation zones and permafrost distribution across a meander on the Chena River, Alaska 53

29 Vegetation zones and interrupted forest succession on a floodplain in northeastern British Columbia ... 54

30 Concentrations of whistling swans staging on the Peace-Athabasca Delta 63

31 Major North American flyways of migratory waterfowl 66

LIST OF FIGURES (Cont'd)

FIGURE		PAGE
32	Flyways of migratory waterfowl in the Mackenzie River Basin	68
33	Influence of water levels on winter survival of muskrat	71
34	Formation of sub-ice space beneath hanging ice ledge in winter	73
35	Meander scroll depressions support stands of poplar which are attractive to beaver	75
36	Willow ptarmigan often use alluvial sites where willow is plentiful in winter and spring	80
37	Grizzly bear with cubs foraging on a braided stream bed which has succeeded to sweet vetch and soapberry	81
38	Alluvial area of willow used by moose for wintering	82
39	Upper reaches of the Athabasca River valley provide wintering habitat for a variety of ungulate species	83

CHAPTER I

INTRODUCTION

Spring break-up and the snowmelt flood are the major hydrological events each year in rivers of the Mackenzie River Basin. Physical and biological processes that are tied to these annual events have a direct bearing on the productivity of alluvial landforms along rivers and streams in the basin. In turn, biological productivity of alluvial sites determines the rate at which renewable resources are produced along rivers in the basin. Waterways of the basin are the focus for a wide range of human uses that collectively exceed the variety of land uses possible further away from the river. Thus, the web of events that are tied to spring break-up have a pervasive relationship to a wide variety of human uses of rivers and their adjacent alluvial ecosystems.

The broad purpose of this report is to document break-up and the snowmelt flood as they relate to vegetation of alluvial sites and to wildlife species that rely upon alluvial habitats along the major rivers of the Mackenzie River Basin. The report deals with hydrologic processes during floods, climatic conditions in relation to flood periods, the life and death of alluvial landforms, plant succession and primary productivity of alluvial sites, wildlife habitat on alluvial sites, and ecological processes in alluvial ecosystems. Some aspects of resource use are discussed. The final chapter is a synthesis of the complex ecological relationships within alluvial ecosystems of the Mackenzie River Basin. The main technical terms used in the text are defined in a glossary at the end of the report.

A. Study Objectives

The terms of reference for the study called for three specific steps:

- assembly of existing biophysical information from the Mackenzie River Basin, as well as from other major northward-flowing rivers in the circumpolar region, and evaluation of this information for relevance to the study;
- synthesis of information on relationships between physical and biological components of northern alluvial habitats, with particular attention to alluvial sites in the Mackenzie River Basin;
- analysis and description of ecological processes involved in the natural creation, maintenance and loss of plant communities and wildlife habitats in the Mackenzie River Basin.

The overall goal was to summarize scientific studies that have revealed the main features and processes connecting spring break-up with alluvial ecosystems. Where the experience of the authors or their interpretations of scientific literature could contribute to the discussion, such additional information was added to the information available from the technical literature. Although this required a number of individual subjects to be reviewed in considerable detail as though each of them was a distinct topic of primary concern, the ultimate goal was to identify and describe ecological relationships between physical and biological processes within alluvial ecosystems. There was an attempt to reach this goal within several of the individual technical chapters of the report, but it is mainly the synthesis of ecological processes (Chapter VII) that focuses on cause-effect relationships within alluvial ecosystems of the Mackenzie River Basin.

The area of geographic coverage for this study included all of the Mackenzie River Basin (Figure 1). Within individual valleys, the area of interest extended laterally to the upper limit of alluvial deposits, including ancient terraces that are now well above the level of the most extreme recorded floods. Non-alluvial upland sites were discussed where this was necessary to account for wildlife life cycle or habitat relationships and where deliberate comparisons were made between alluvial and non-alluvial sites. Alluvial fans were not included in the review of ecological information. Alluvial fans are somewhat analagous to deltas, in the sense that they are built mainly during floods. The most conspicuous alluvial fans are formed where streams with heavy silt loads emerge from hills or mountains onto a lowland; they are therefore particularly abundant in western portions of the Mackenzie River Basin. Since alluvial fans in mountainous terrain are generally beyond the potential zone of influence of major streams of the basin, ecological relationships on fans were excluded from the synthesis presented in the following chapters.

Certain subjects for which there are extremely limited data specifically from alluvial sites in the Mackenzie River Basin were reviewed from a broader geographic area. For example, comparisons of nutrient content of vegetation from alluvial and non-alluvial sites, as well as comparisons of primary and secondary productivity on flood-prone areas and nearby upland areas, required the interpretation of some information from ecological literature for areas beyond the Mackenzie River Basin. For ecological subjects of a theoretical nature, the summarized information was not necessarily derived from studies in northern alluvial systems. Wherever possible, however, information on fluvial and biological processes was derived from drainage basins that were judged to have considerable climatic, hydrologic and ecological similarities to the Mackenzie River Basin. Information derived from study sites outside of the basin was mainly from the Colville and Yukon rivers in Alaska, the Saskatchewan-Nelson river system and the Lena, Ob, and Yenisey rivers of the Soviet Union.

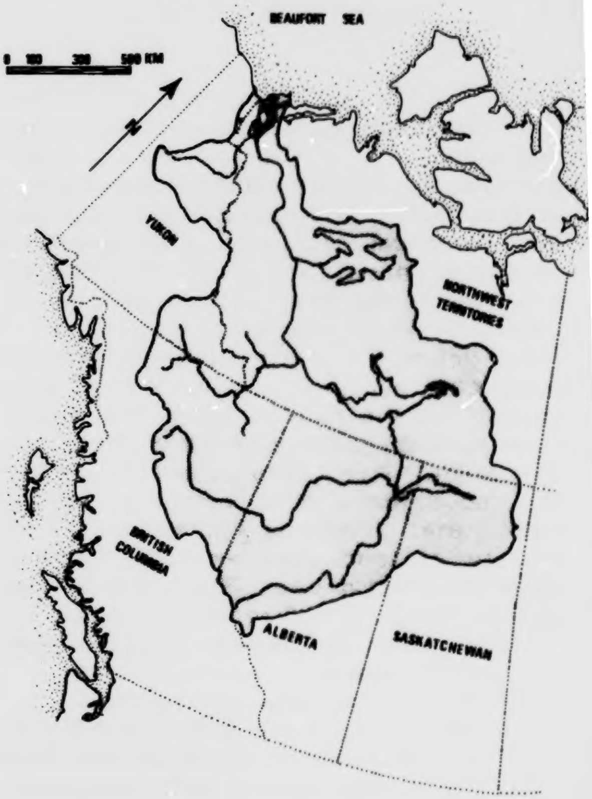

Figure 1. THE MACKENZIE RIVER BASIN

B. The Mackenzie River Basin

The Mackenzie River Basin (Figure 1) drains one-fifth of the total area of Canada and its area of almost 2 000 000 km^2 makes it one of the world's largest river systems. In a Canadian context, the Mackenzie River system has both the largest drainage area and greatest river length, flowing approximately 4 000 km from the Finlay River headwaters in British Columbia to the Beaufort Sea. The basin occupies parts of three provinces and two territories (Inland Waters Directorate 1973).

In the chapters that follow, "Mackenzie River" refers to that part of the system that extends from Great Slave Lake to the Beaufort Sea. The three main tributaries within the basin are the Peace, Athabasca, and Liard rivers (Figure 2). The larger tributaries of the Mackenzie downstream from the Liard River confluence are the Great Bear, Arctic Red and Peel rivers.

One of the special features of the Mackenzie River Basin is the presence of three major deltas, two of which are inland (Peace-Athabasca Delta and Slave Delta) and one of which is coastal (Mackenzie Delta).

The focus in the report is on hydrological and ecological conditions as they exist today in the Mackenzie River Basin. Since only the Peace River and Lake Athabasca sub-basins have been influenced by storage structures or water level control measures, the chapters that follow are essentially an account of natural hydrological and ecological conditions associated directly or indirectly with spring break-up. In the case of the Peace River and the Peace-Athabasca Delta, conditions described in this report are those that exist after several years of regulated flow.

Water flows in the Peace River and levels of Lake Athabasca were affected by closure of the W.A.C. Bennett Dam in 1968 and filling of Lake Williston from 1968 to 1971. Remedial measures on the Peace-Athabasca Delta included a temporary rockfill weir on the Quatre Fourches Channel from 1972 to 1975 and permanent weirs built on the Riviere des Rochers and Revillon Coupe in 1975. The effects of specific flow regulation measures are discussed in the report in relation to vegetation and wildlife changes on the Peace-Athabasca Delta.

Names of rivers and settlements that are referred to in the report are shown for the Mackenzie River Basin in Figure 3 and for individual delta areas in Figures 5, 6 and 7.

C. Spring Break-up and Other Special Features of Northern Rivers

Although northern rivers exhibit depositional and erosional processes much the same as rivers anywhere else, scientists who specialize in river studies have identified several specific features associated with severe low temperature, seasonal occurrence of ice and presence of permanently frozen ground.

One of the key features of northern and mountainous areas, such as in the Mackenzie River Basin, is that for much of the year precipitation remains on the ground as snow. The effect of spring melting, as far as runoff is concerned, is to redistribute six to ten months of precipitation as if it had all occurred during the short snowmelt period. The short, concentrated period of runoff is considered by some hydrologists to be the most important feature of the hydrological cycle in the north (Church 1977).

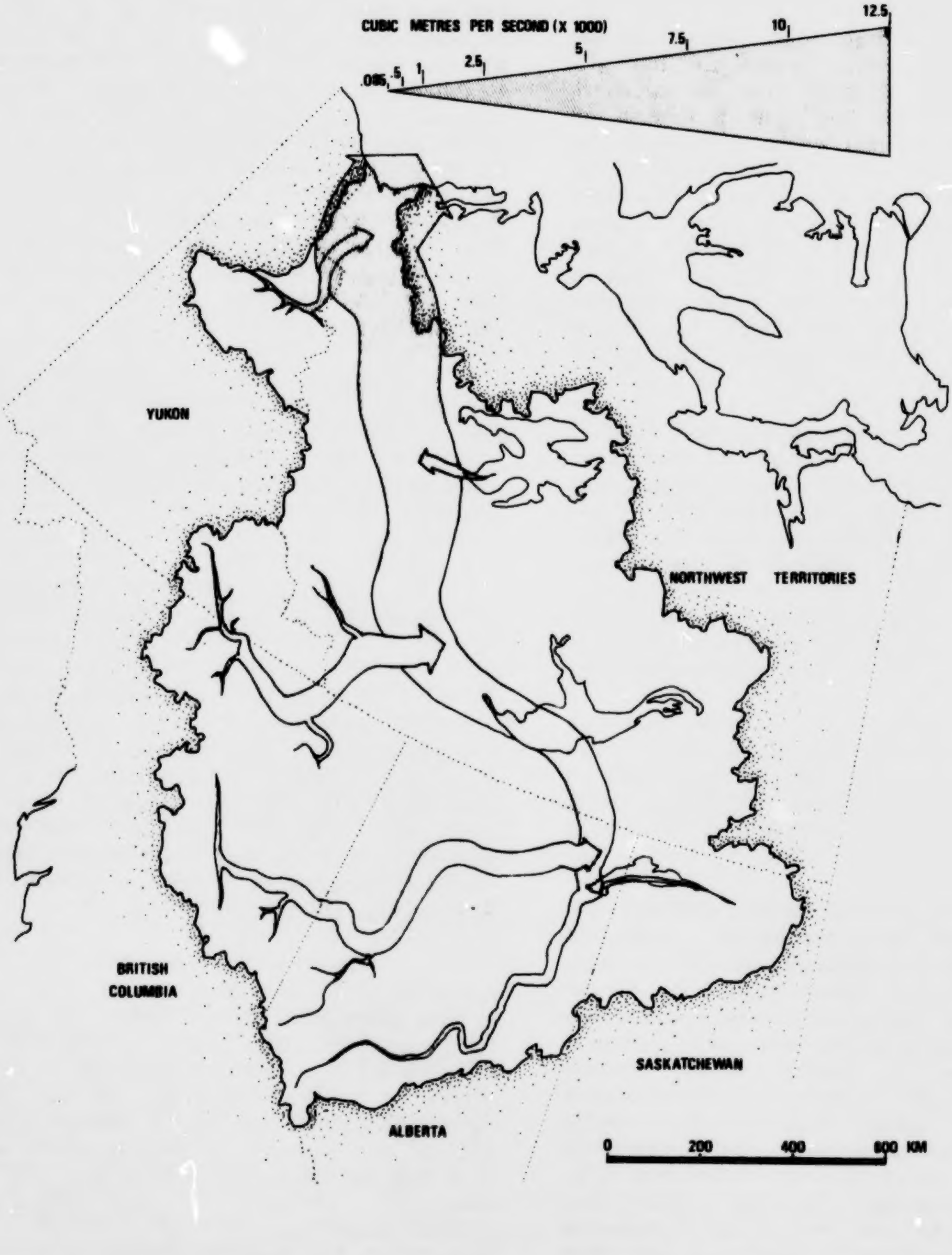
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Figure 2. MEAN ANNUAL FLOW OF MACKENZIE RIVER AND ITS MAIN TRIBUTARIES (adapted from Fisheries and Environment Canada 1978)

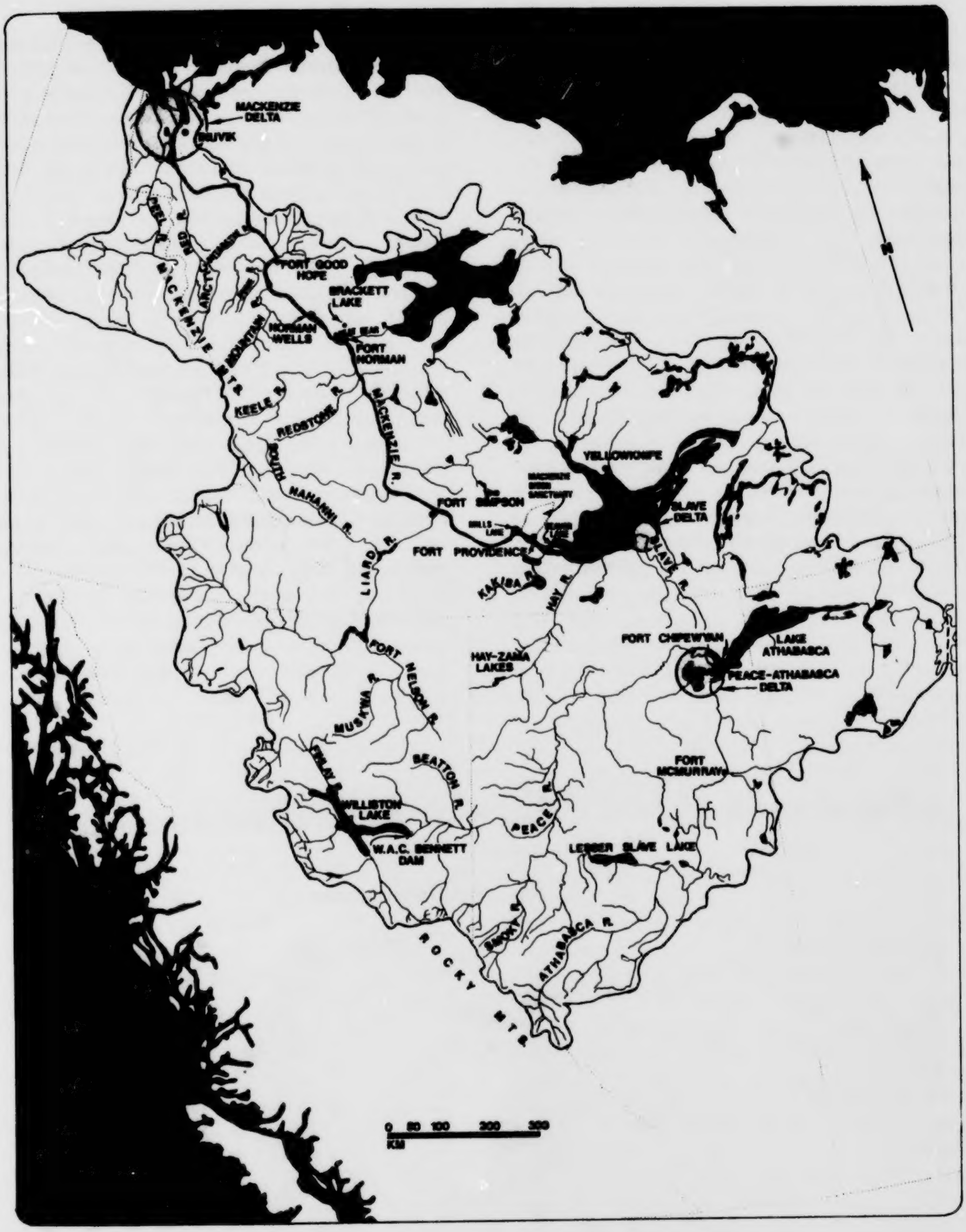
MACKENZIE DELTA
INUVIK
PEEL R.
MACKENZIE MTS
ARCTIC RED R.
FORT GOOD HOPE
BRACKETT LAKE
NORMAN WELLS
FORT NORMAN
MOUNTAIN R.
KEELE R.
REDSTONE R.
SOUTH NAHANNI R.
MACKENZIE R.
FORT SIMPSON
MACKENZIE BISON SANCTUARY
MILLS LAKE
BEAVER LAKE
FORT PROVIDENCE
YELLOWKNIFE
SLAVE DELTA
SLAVE R.
LIARD R.
KAKISA R.
HAY R.
FORT CHIPEWYAN
LAKE ATHABASCA
PEACE-ATHABASCA DELTA
HAY-ZAMA LAKES
FORT NELSON R.
MUSKWA R.
FINLAY R.
BEATTON R.
WILLISTON LAKE
W.A.C. BENNETT DAM
PEACE R.
FORT MCMURRAY
LESSER SLAVE LAKE
SMOKY R.
ATHABASCA R.
ROCKY MTS
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Figure 3. RIVER AND SETTLEMENT PLACE NAMES USED IN THE TEXT, MACKENZIE RIVER BASIN

Another reason for the dominance of spring break-up and the snowmelt flood in the annual hydrograph pattern of discharge in most streams of the Mackenzie River Basin is that there is no strong influence of summer-long runoff from glacier melt. Streams that are fed by glacier meltwaters have distinctive daily discharge characteristics, with discharge being dependent upon incoming solar radiation in the glacier area from early July onwards during the summer. Discharge by glacial meltwater in late summer tends to reduce the relative dominance of spring snow-melt water levels in streams close to glaciers. However, the proportion of glacier derived water to non-glacial water decreases as one goes downstream from glaciers. As a result, even though the Mackenzie River Basin contains many glacier-fed headwater areas, the Mackenzie River itself is so far from glaciers that the river's hydrograph is influenced little by their meltwater contributions in late summer. The size of the basin also lessens the potential influence of catastrophic floods that may occur within the headwater areas of watersheds as a result of sudden release of ice-dammed or debris-dammed lakes at glacier margins (Church 1977). In general, glacier-related floods are not a major phenomenon in the Mackenzie River Basin where spring break-up (Figure 4) reigns as the dominant hydrological event each year (Church 1977).

The presence of large volumes of ice can be a factor of particular importance for flooding. For example, in many channels of the basin peak water levels due to freeze-up (frazil) ice jams or due to break-up ice jams frequently exceed snowmelt flood water levels. In other channels, including many of the major tributaries of the Mackenzie River, break-up is dominated by local melting of river ice in place with few ice jams and few major ice runs. Break-up ice jams tend to occur where there are channel bends,

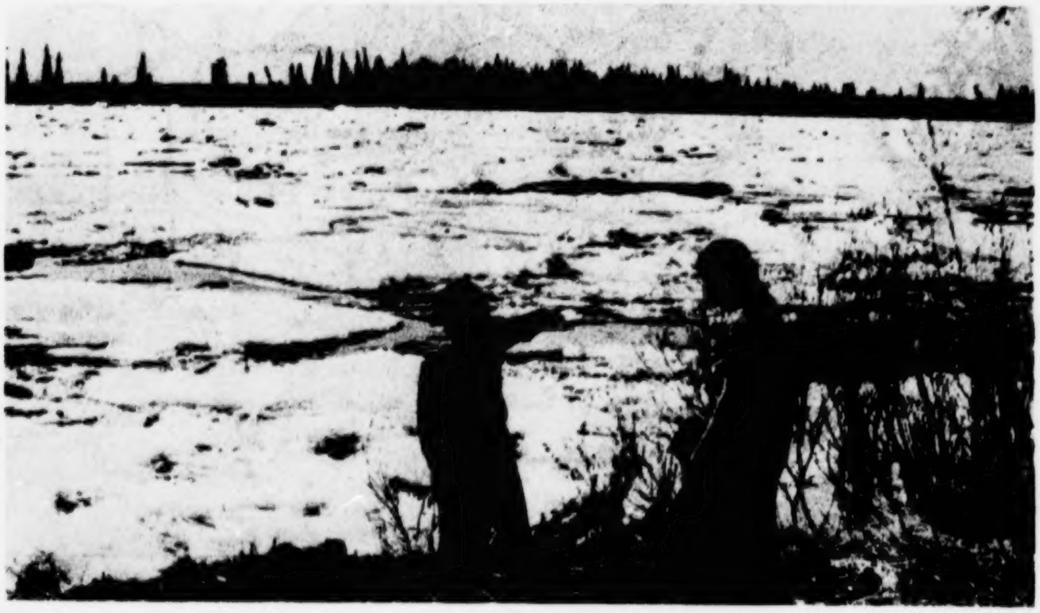

Figure 4. SPRING BREAK-UP ON THE MACKENZIE RIVER (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

confluences or channel islands. Within the Mackenzie River Basin, a key hydrological feature in spring is the northward movement of a flood wave that is the main force behind the massive break-up ice jams of the Mackenzie River below the outlet of the Liard River. As one moves north within the basin, the spring peak of water levels and break-up become more closely associated in time; in contrast, in the southern part of the basin at Peace River, Alberta, peak water levels and break-up are separated by more than a month (R. Kellerhals, pers. comm. 1981).

Drainage of the basin from north to south creates other important features, most notably an earlier breakup in the southern part of the basin than in the northern parts. One consequence of this feature is that relatively warm water is injected into a colder environment as runoff water moves north.

In addition to spring break-up, several other features of northern areas impart special characteristics to subarctic rivers. In general, such rivers experience low summer flows punctuated by rainstorm floods which may exceed the spring freshet, especially on rivers with mountainous headwaters.

Perennially frozen ground has a variety of effects on both river hydrology and channel stability in northern rivers. Effects of permafrost include: an increase in the proportion of surface runoff to total runoff; retardation of bank erosion over short time spans; and an increase in the relative importance of block slumpage in channel migration (McDonald and Lewis 1973). In general, perennially frozen ground restricts exchanges between surface water and groundwater below the perennially frozen layer. A perched water table commonly develops during summer above frozen ground, with standing surface water a frequent result.

Standing surface water contributes to development of muskeg vegetation in subarctic regions. Zoltai (1979) showed that peatlands cover large portions of the basin, estimated at 530 000 km^2. However, about half of the peatlands in the basin are perennially frozen and are unaffected by seasonal water fluctuations. Floodflows are generally reduced in watersheds that have large areas of peaty land types because of the large water-holding capacity of muskeg; the water storage effect of large areas of peat-dominated vegetation is comparable to that of lakes (Church 1977). However, if snowmelt and prolonged rain fill the water storage capacity of a peat-dominated basin, as they occasionally do, additional rain can result in outstandingly large runoff rates and extreme floods. Under such conditions the basin suddenly performs as if it were mostly impervious (R. Kellerhals, pers. comm. 1981).

Channel icings occur when a channel is too shallow, or has too little flow, to permit formation of a normal ice cover. The channel freezes to the bottom and the remaining flow is forced up through cracks in the ice. The channel can be filled with ice and even the adjacent floodplain may be ice-covered. During snow-free cold periods, channel icings have been observed as far south as southern British Columbia and they are common within the Mackenzie River Basin. Processes associated with channel icings lead to a distinct channel morphology of many small northern streams (Kellerhals and Church 1980).

Natural flow regimes on rivers in the Mackenzie River Basin are characterized by extremely variable monthly distributions of runoff, particularly in tributaries of the Mackenzie River and in more southerly parts of the basin (Energy, Mines and Resources Canada 1974). The Peace and Liard rivers derive most of their flow from mountainous areas where natural storage is limited and in these sub-basins ratios of maximum to minimum flows of 50 to 100 are common. In contrast, in the Mackenzie River upstream from the Liard River junction there is a large capacity of lake storage with the result that ratios of maximum to minimum flow drop below 5 (Kellerhals and Gill 1973).

Later sections of the report provide examples that show how alluvial landforms, vegetation, wildlife and certain aspects of renewable resource harvesting are adapted to the flow variation and other physical changes caused by the annual spring break-up. Ecological consequences of high summer discharges during rain storms, which may exceed spring discharge rates, are also discussed.

D. Major Deltas in the Mackenzie River Basin

The Mackenzie River Basin is unique among large drainage areas of Canada because it contains three major deltas - the coastal delta of the Mackenzie River and the inland Peace-Athabasca and Slave deltas. Partly because of the sheer physical prominence of these deltas and partly because of the flood-related processes that are specific to deltas, the distinction between deltaic and non-deltaic alluvial sites is emphasized, where appropriate, in the subdivision of several chapters of the report.

The Peace-Athabasca Delta (Figure 5) is the most southerly of the three major deltas in the basin. Formed of the combined deltas of the Peace and Athabasca rivers, the total delta complex occupies an area of about 6 070 km^2 (the Peace-Athabasca Delta Project Group, 1972), of which 1 968 km^2 is designated as the Athabasca Delta, 1 683 km^2 as the Peace Delta, 168 km^2 as the Birch Delta (Bayrock and Root 1973) and the remainder as water surfaces. The latter is made up mainly of Lake Claire, Mamawi Lake, Baril Lake and Richardson Lake. This large inland delta was laid down by the Peace and Athabasca rivers, with contributions from the Birch River, in post-glacial Lake Athabasca. At present, the Athabasca River is actively extending its delta into Lake Athabasca and the southern portion of the Peace-Athabasca Delta is dominated by fluvial processes of the Athabasca River. The northern portion, the delta of the Peace River, is in an old stage of development, effectively inactive, because the river flow normally by-passes the delta. Sediments from the Peace River are now added to the Peace-Athabasca Delta only during high flood stages (Bayrock and Root 1973).

Under natural conditions, direction of flow in channels that connect the Peace River with Lake Athabasca depended on relative levels of the river and lake. When water levels on the delta and Lake Athabasca are high, the channels drain to the north, out of the delta. When the Peace River floods, or is backed up by major ice jams, so that it is higher than Lake Athabasca, the channels drain to the south, from the river into the delta. Weirs in the Riviere des Rochers and Revillon Coupe allow floodwater of the Peace to enter Lake Athabasca and the delta, but restrict outflow from the lake. The main effect of the weirs is to prevent the lake from receding quickly to lower than natural levels. Floods are no longer as high as they were prior to regulation of the Peace River, because of the primary effect of the W.A.C.

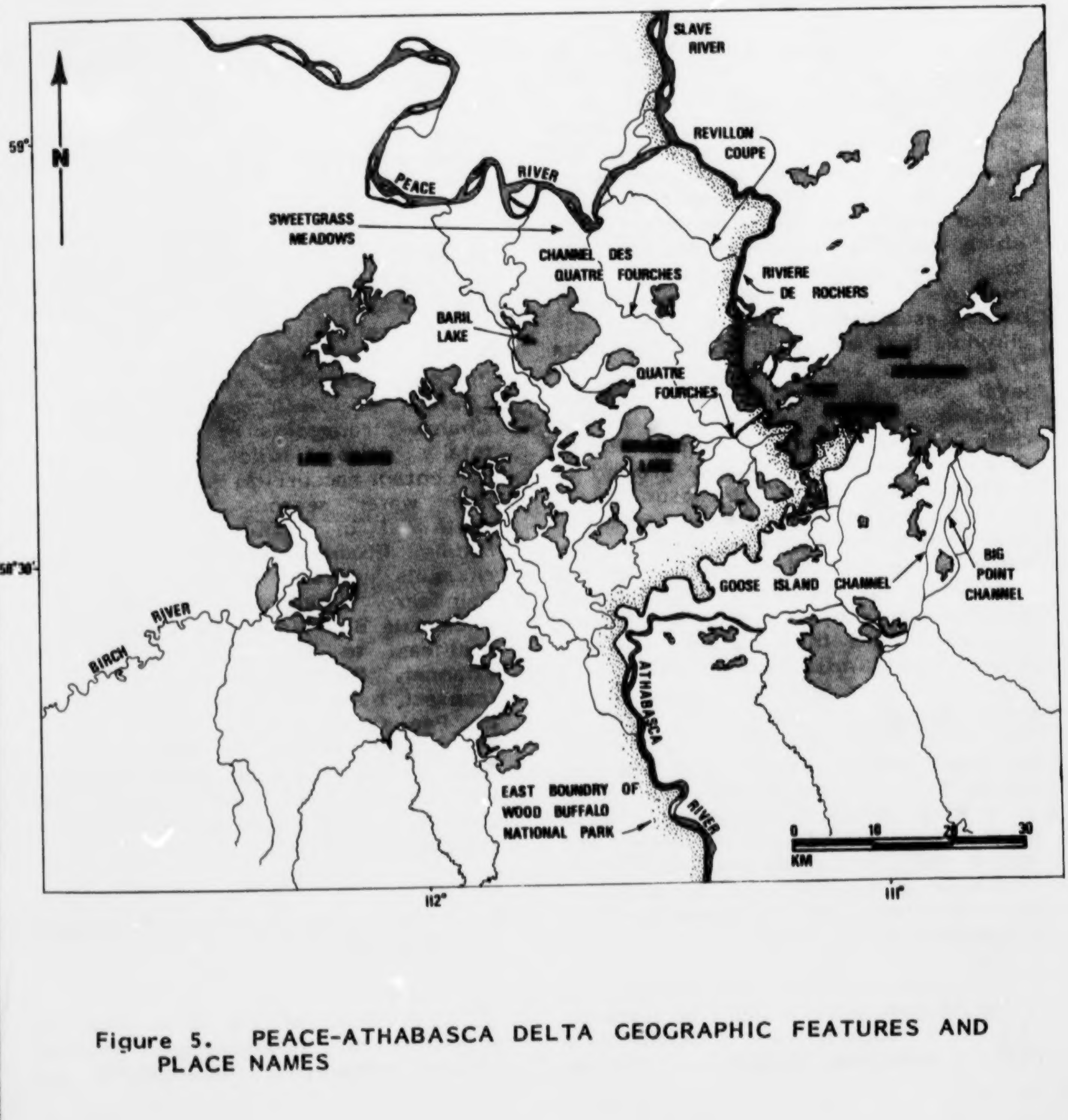
SLAVE RIVER
N
59°
REVILLON COUPE
PEACE RIVER
SWEETGRASS MEADOWS
CHANNEL DES QUATRE FOURCHES
RIVIERE DE ROCHERS
BARIL LAKE
QUATRE FOURCHES
58°30'
GOOSE ISLAND CHANNEL
BIG POINT CHANNEL
BIRCH RIVER
ATHABASCA RIVER
EAST BOUNDRY OF WOOD BUFFALO NATIONAL PARK
0
10
20
30
KM
112°
111°

Figure 5. PEACE-ATHABASCA DELTA GEOGRAPHIC FEATURES AND PLACE NAMES

Bennett Dam. The frequent formation of ice dams in the Peace and Athabasca rivers adds to the complexity of hydrological and ecological processes in this delta. Unlike the Mackenzie and Slave deltas, the Peace-Athabasca Delta contains two large, shallow lakes (Mamawi and Claire). Permafrost is generally lacking in the Peace-Athabasca Delta.

The Slave Delta (Figure 6) occupies an area of 310 km^2, approximately 200 km downstream of Fort Smith, where the Slave River enters Great Slave Lake. It lies within the Slave River Lowlands, a physiographic unit that Day (1972) identified as a former south arm of Great Slave Lake which was filled by sedimentation. As the lake receded during the post-glacial period, the Slave River became established. Today, most of the alluvium that makes up the active delta is less than 3 m above average river level and is subject to frequent flooding. In more stable parts of the delta, particularly along Nagle Channel, perennially frozen ground is present below 80 cm (Thompson et al. 1979), but less stable sites generally lack perennially frozen ground in this delta. As in other deltas, spring floodwaters on the Slave Delta deposit alluvium, re-supply water to perched basins and aid the dilution of acidic organic compounds. Spring floodwaters result in formation of levees along major channels of the delta. Behind the levees occur alluvial lowlands with occasional oxbow ponds and perched basins that require flooding to retain their water levels. The natural growth of the delta is into Great Slave Lake where silt is deposited, but this deposition is counteracted by sediment loss from wave action and lake currents (Thompson et al. 1979).

The Mackenzie Delta (Figure 7) is the largest modern delta in Canada. The word 'modern' refers to the fact that the delta was formed since retreat of the last continental glaciation; in contrast, the higher area just east of the present delta is referred to as a Pleistocene delta (Heginbottom 1973). The Mackenzie Delta extends approximately 200 km from Point Separation north to the Beaufort Sea, and 65 km from the Richardson Mountains eastward to the Caribou Hills and the Pleistocene delta of Tuktoyaktuk Peninsula. The modern delta is an estuarine deposit built from sediments delivered mainly by the Mackenzie and Peel rivers. The Rat and Rengleng rivers and Caribou and Frog creeks are other drainages that enter the delta perimeter.

Surface water coverage exceeds 25% over much of the area of the Mackenzie Delta. Water surfaces are represented by an intricate network of channels, inter-levee basins, and lakes. Within the delta, most of the incoming water is carried by Middle Channel. Below Horseshoe Bend, Middle Channel transports 80% to 95% of the total delta inflow, the lower percentages occurring during the summer high water season. About 10 km southwest of Tununuk, flow of the Middle Channel divides into three channels: west to Shallow Bay via Reindeer Channel; northwest to Mackenzie Bay via Middle Channel; and northeast to Kugmallit Bay via East Channel. Of the channels that cross a transect between Inuvik and Aklavik, the Peel Channel at Aklavik is next to the Middle Channel in volume of flow; from 2% to 7% of all delta discharge was observed to pass through Peel Channel during a one-year study period (Heginbottom 1973).

E. Flood-prone Areas as Biophysical Systems

Some of the best scientific accounts of relationships between climatic, geomorphic, vegetational, and

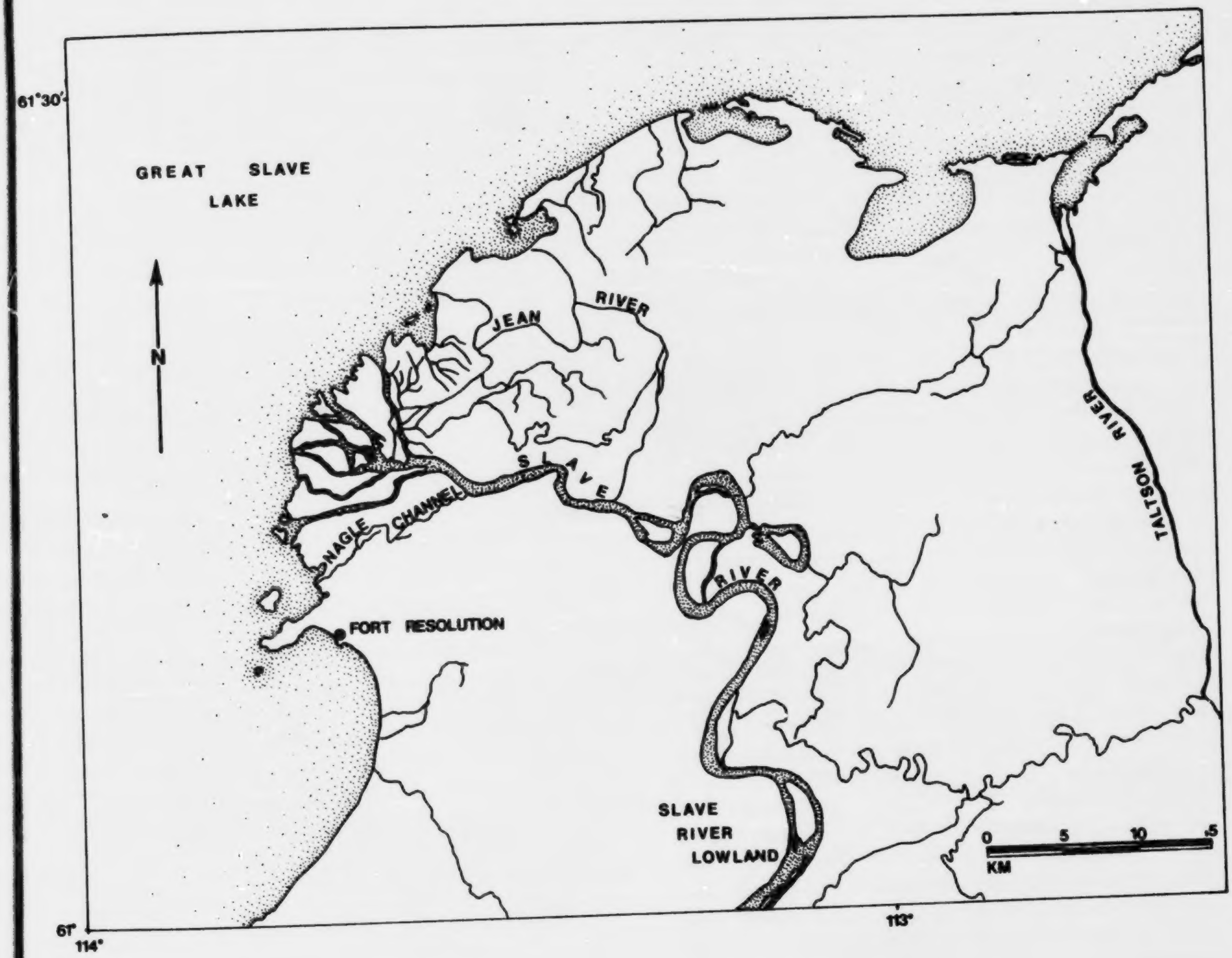
61°30'
GREAT SLAVE LAKE
N
JEAN RIVER
SLAVE RIVER
NAGLE CHANNEL
FORT RESOLUTION
TALTSON RIVER
SLAVE RIVER LOWLAND
0 5 10 15
KM
61°
114°
113°

Figure 6. SLAVE DELTA GEOGRAPHIC FEATURES AND PLACE NAMES

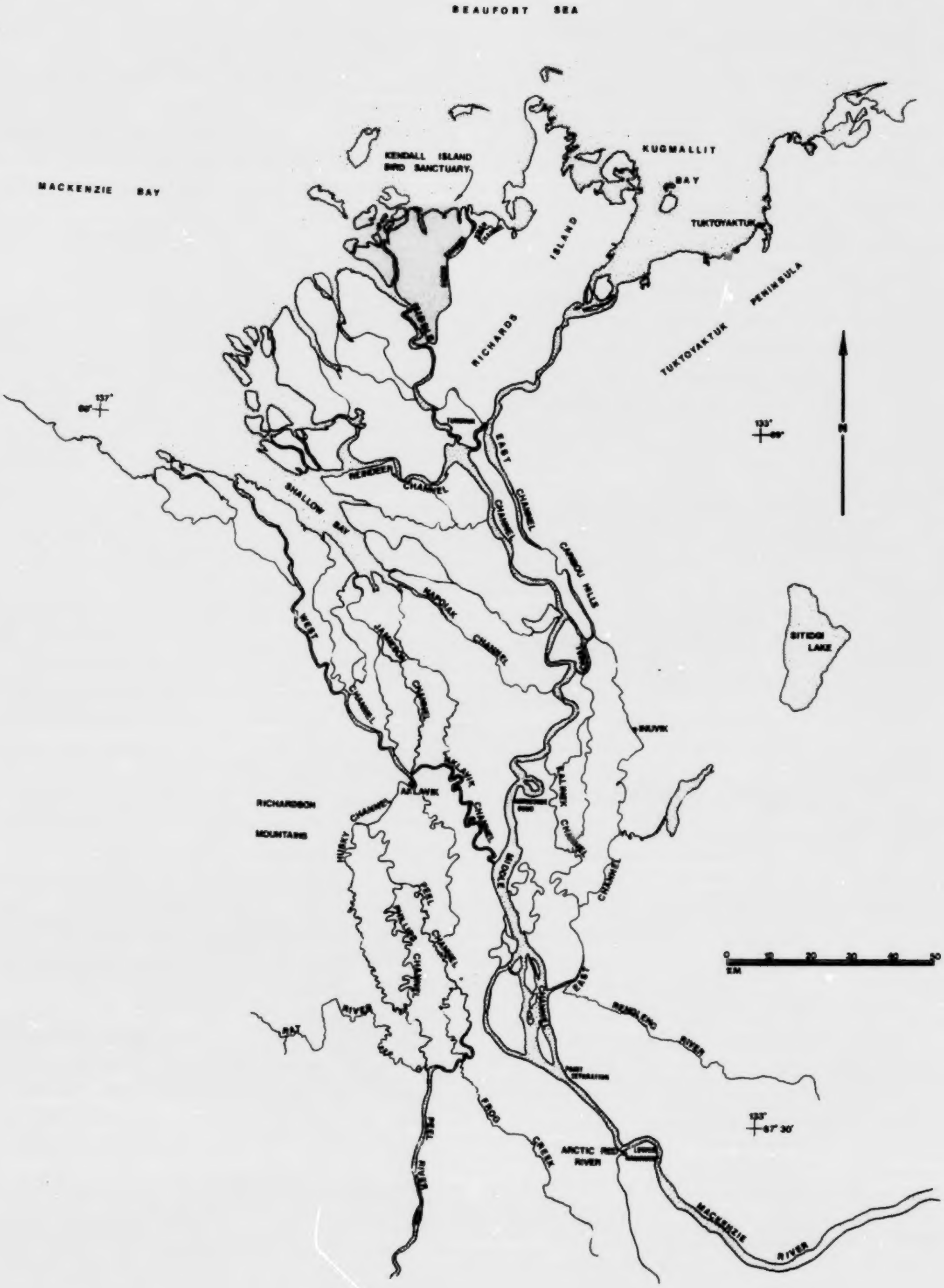
BEAUFORT SEA
MACKENZIE BAY
KENDALL ISLAND
BIRD SANCTUARY
KUGMALLIT
BAY
TUKTOYAKTUK
TUKTOYAKTUK PENINSULA
RICHARDS
ISLAND
137°
69°
133°
69°
N
EAST
CHANNEL
REINDEER
CHANNEL
SHALLOW
BAY
CARIBOU HILLS
NAPOIAK
CHANNEL
SITIDGI
LAKE
WEST
CHANNEL
JAMESON
CHANNEL
INUVIK
AKLAVIK
AKLAVIK
CHANNEL
RICHARDSON
MOUNTAINS
HUSKY
CHANNEL
MIDDLE
CHANNEL
KALINEK
CHANNEL
PEEL
CHANNEL
PHILLIPS
CHANNEL
0
10
20
30
40
50
KM
EAST
CHANNEL
RENGLENG
RIVER
RAT
RIVER
POINT
SEPARATION
PEEL
RIVER
FROG
CREEK
133°
67° 30'
ARCTIC RED
RIVER
MACKENZIE
RIVER

Figure 7. MACKENZIE DELTA GEOGRAPHIC FEATURES AND PLACE NAMES

wildlife components of biophysical systems have resulted from studies in delta areas. A goal of this report is to draw examples from the experience and research of such studies to demonstrate how deltas and other flood-prone areas can be viewed as dynamic biophysical systems in which conditions at any given time are a net result of physical and biological processes. Achieving such a broad goal for an area as large as the Mackenzie River Basin demanded some specific features or event upon which the diverse ecological processes could be focussed; as outlined previously, the selected focus is the spring break-up period and associated floodwaters. This focus did not severely limit the range of ecological subjects discussed because floodwaters serve not only as the architect, builder, and wrecker of alluvial landforms but also as the main supplier of energy, nutrients, and rooting media for vegetational development which, in turn, facilitates a wide range of uses by birds, aquatic and terrestrial furbearers, and ungulates.

It would require a lengthy account to actually describe all of the known biophysical relationships in alluvial ecosystems of the Mackenzie River Basin. Instead of presenting a voluminous inventory of biophysical subdivisions within flood-prone areas of the basin, the approach here was to present enough examples to allow the reader to visualize some of the complex interconnections between climatic, geomorphic, and biological processes.

Only a few scientists have attempted such an integrated approach in their collection and interpretation of data. Within the Mackenzie River Basin, this approach was exemplified by the researchers who contributed to the Peace-Athabasca Delta studies and by the studies of Dr. Don Gill and co-workers in the Mackenzie Delta. Outside of the basin, Maddock (1976) emphasized that the boundaries of a stream channel - the bed and banks - offer an excellent opportunity to demonstrate how processes interact to form a biophysical system. Vegetation serves as a link between physical processes and wildlife use of alluvial habitats, and alluvial vegetation is strongly influenced by physical conditions on the bed and banks of stream channels. Therefore, the degree of movement of alluvial materials that make up the channel boundaries, and the time of year that this movement takes place, have a considerable influence on development, longevity, and productivity of alluvial systems.

The degree to which vegetational development and fluvial processes are biophysically inter-related is indicated by the frequent use of botanical evidence in the study of floods and floodplain deposition. Dendrological methods used to determine dates and occurrences of floods and deposition of sediment on modern floodplains include analyses of: annual ring growth around trunk scars; growth of sprouts from water-felled trees; growth of trees following burial by alluvium; relationships between floodplain trees and low flow; and significance of old trees on banks (Sigafoos 1964). Trees can also be used to determine the recent history of channel migration and floodplain construction because forests near channels are often composed of a series of even-aged bands of trees that show an orderly increase in age up-valley and away from the channel. Each forest band is apparently the result of a rise of a sapling thicket on a riverside sandbar, and thus the forest can be used as a living record of recent migration of the channel (Everitt 1968). Such successional sequences are complicated by events in areas where ground ice can develop. For example, the gradual development of permafrost into former root zones of previously unfrozen soils of the willow-horsetail vegetation type in the Mackenzie Delta has been documented by Gill (1973a). The formation and decay of perennially frozen ground in the Mackenzie Delta is a dynamic process that involves major areal displacement of permafrost bodies through time and there are close relationships between the distribution of certain plant communities and the thermal characteristics of underlying soils.

CHAPTER II

HYDROLOGIC FEATURES RELATED TO GEOMORPHIC AND VEGETATIONAL PROCESSES

It is not the purpose of this report to describe in detail the hydrology of the Mackenzie River Basin. Attention is given only to selected hydrologic topics, especially processes directly related to floods and to other processes that influence vegetational development and wildlife use of alluvial sites during periods between floods. The two major subdivisions of the chapter focus on: processes during flood periods that are thought to have the most direct relationships with vegetation or wildlife, and; hydrologic processes during non-flood periods in relation to vegetational change and wildlife use on alluvial sites.

Reports reviewed in this chapter deal almost entirely with studies from within the Mackenzie River Basin. Other study reports from within the basin that were reviewed for background material, but not summarized here, include: Beltaos 1978; Church and Kellerhals 1979; Egginton 1980; Gerard 1975; Neill 1965; and Sampson 1973. Other reports reviewed for study areas outside of the basin included: Branson 1975; Burdykina 1970; Dupre and Thompson 1979; Leopold and Langbein 1966; Maddock 1976; Newbury 1974; Sigafoos 1964; Slaughter and Bilello 1978; Walker 1974 and Woodward-Clyde Consultants 1980.

A. Hydrologic Processes Important for Alluvial Vegetation and Wildlife During Floods

In the Mackenzie River Basin there are four distinct types of floods: flooding related to break-up ice jams; flooding as a result of snowmelt, referred to here as the snowmelt flood but sometimes called the spring flood; flooding due to summer storms; and floods associated with frazil ice accumulation at freeze-up. Although the snowmelt flood receives most attention in hydrologic descriptions of the basin, summer floods also exert a significant control over vegetational development in flood-prone areas. Wherever appropriate, the discussions below maintain a distinction between the various types of floods. The distinction of different types of floods in the Mackenzie River Basin is particularly significant for parts of the basin southwards from the Peace-Athabasca Delta.

1. Flooding During Spring Break-up: Features of the snowmelt flood that are of particular ecological significance are its timing, magnitude, interactions with river ice and spreading of alluvium on the floodplain.

a. Spring break-up in the Mackenzie River Basin: In the southern part of the Mackenzie River Basin, spring break-up occurs on the Fort Nelson River in late April and early May, during which time sediment load greatly increases on the Fort Nelson River. This river serves as the main source of suspended sediment to the Liard River. Above Nelson Forks, on the Liard River, suspended sediment discharge peaks in early to mid-June with the snowmelt flood (Grey and Sherstone 1980).

Ice break-up on the Mackenzie River, as in other arctic rivers, is associated with a rapid rise in water level. Records of water level are not available for the Mackenzie River at the time of ice break-up but they are available at Fort Simpson soon after break-up. From Fort Simpson records between 1961 and 1968, it is clear that there is a correlation between high water levels and rapid ice clearance (MacKay and Mackay 1973a). In general, the timing of ice clearing has a fairly close relationship to timing of the snowmelt flood.

There is a rapid rise in water level during break-up because there is a certain amount of water stored in ice-covered rivers and this water is released during break-up. In river systems such as the Athabasca, Peace or Liard, where break-up tends to occur in the downstream direction, break-up in the headwater region produces a flood wave by releasing stored water. This wave, which is generally much smaller than the spring snowmelt flood, helps to break up the ice along more northerly reaches where ice may still be relatively solid (R. Kellerhals, pers. comm. 1981).

The Mackenzie River does not break up sequentially from south to north. Upstream of the Liard River confluence with the Mackenzie River, ice break-up is delayed because of a steady outflow of cold water from Great Slave Lake. Therefore, above the Liard River confluence, the Mackenzie River breaks up when warm weather has weakened the ice sufficiently to permit break-up; this gradual process is referred to as thermal break-up and it is not accompanied by a significant increase in flow. In contrast, below the Liard River confluence, there is primarily mechanical break-up because the spring flood wave out of the Liard River lifts, breaks and moves an ice cover that is often still very sound (Kellerhals and Church 1980).

Below Fort Good Hope, ice break-up is relatively late because there are no major tributaries to add to water levels in the Mackenzie River, and also because of delayed melting due to lower temperatures associated with the more northerly location. Break-up of ice around Inuvik is typically two to three weeks behind the mid-May break-up between Fort Simpson and Fort Good Hope.

b. Areas subject to most severe flooding in spring: The Liard River snowmelt flood has received considerable study because the Liard River Basin is the main contributor of suspended sediment to the Mackenzie River and because the Liard River is responsible for break-up of the Mackenzie River. Unlike the Athabasca and Peace rivers, where flows are regulated by passage through Lake Athabasca and Great Slave Lake, the Liard River's discharge encounters no such storage delay from large lakes (Grey and Sherstone 1980). The Liard River is the prime force behind ice break-up on the Mackenzie River between Fort Simpson and Fort Good Hope (MacKay and Mackay 1973a) but there is not a spectacular break-up on the Liard River every year. For example, Grey and Sherstone (1980) documented the 1979 flood in which there were several sections of the river where ice cover simply melted in place over a period of several days. Although there was a high frequency of ice dams in 1979 on the Liard River, no major flooding from ice jams occurred (Grey and Sherstone 1980).

Ice movement is often triggered on a river at the confluence with a tributary. For example, high flows from the Fort Nelson River serve to initiate ice movement in the Liard River below the confluence, just as Liard River outflow initiates ice movement on the Mackenzie River below Fort Simpson (Grey and Sherstone 1980).

Measured upper limits of ice-shove or driftwood along the Mackenzie River indicate the maximum level of break-up flooding on the river (MacKay and Mackay 1973a). The most consistent high flooding occurs between Fort Good Hope and the Lower Ramparts.

The extent of flooding decreases from the Lower Ramparts north to Point Separation at the south end of the Mackenzie Delta. Between Fort Simpson and Fort Good Hope flooding is intermittent (MacKay and Mackay 1973a). Upstream from the Liard-Mackenzie confluence, in the reach between Fort Simpson and Fort Providence, the snowmelt flood peak occurs weeks after break-up. All but one of the observed peak flows at Fort Simpson occurred in June or July (R. Kellerhals, pers. comm. 1981).

Some of the ice jams that cause flooding occur at or directly below tributary junctions. Ice runs from rivers such as the Liard, Nahanni, and Great Bear tend to overload the transport capacity of the Mackenzie River, with resulting ice jams near the tributary junctions (MacKay and Mackay 1973a). Tributary ice runs often encounter a solid ice cover on the main river, especially in tributaries that enter from the south such as the Smoky River entry to the Peace River, the Fort Nelson River entry to the Liard River, or the Liard River entry to the Mackenzie River.

Other features such as narrow channels, sharp bends, mid-channel islands, rock ledges, and shoals may cause a local piling-up and stranding of ice. Distribution of such local pile-ups was found to be fairly consistent from one break-up to the next (MacKay and Mackay 1973a).

2. Ice-Floodwater Interactions: River ice creates ice jams at certain locations along river channels and ice-shove zones along many channel stretches (MacKay and Mackay 1973b). Not surprisingly, river ice has some profound physical effects upon any vegetation that becomes established below the level of maximum ice-shove. Ice-related aspects of floodwaters are outlined below.

a. Ice jams in the Mackenzie River Basin: Aside from the rapid rise in water level, the most dramatic effects of spring break-up are associated with ice jams and ice-shove processes. Although many ice jams occur during spring break-up, Henoch (1973) noted that, in some years, ice flows coming out of Great Slave Lake build an ice jam at Fort Providence at freeze-up. Ice jams at freeze-up, involving frazil ice, are very common along some river reaches in the Mackenzie River Basin; in the Peace River below the W.A.C. Bennett Dam frazil ice jams persist all winter now and have caused widespread damage (R. Kellerhals, pers. comm. 1981).

MacKay and Mackay (1973a) listed several ice-related processes that are set in motion by high water levels of the break-up period, including impoundment of water upstream from ice jams, construction of terraces by the dual action of ice shove and sedimentation, stranding of driftwood at all levels on the river bank, and formation of boulder pavement (Figure 8) in constricted parts of the

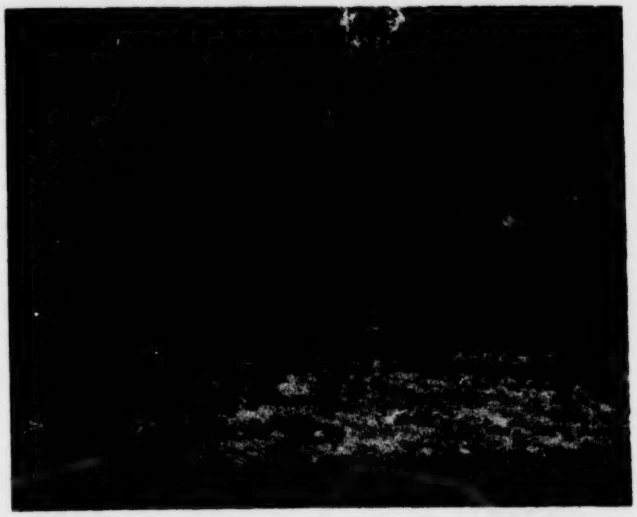

Figure 8. BOULDER PAVEMENT IN ICE-SHOVE ZONE AT CHANNEL MARGIN (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

channel. Driftwood on banks of the Mackenzie River is a commonly used indicator of maximum flood level (Figure 9), generally as a result of ponding behind ice dams but occasionally as a result of high water levels during summer storms.

b. Ice-shove zones: Maximum flooding level and maximum ice-shove level are not necessarily synonymous. Where the flow of ice is free, the height at which ice rafts are deposited, and the height of ice scars on trees, does tend to coincide with the height of flooding. However, Henoch (1973) documented ice rafts that are pushed onto channel banks where they form distinct ridges (Figure 10). This happens particularly where the flow of ice is hindered by a channel bend or by an island. Injuries to the bark of trees growing on river banks are used as indicators of maximum ice-shove levels. Such bark injuries can also be used to date ice-shove damage because the scars heal over and are surrounded by tree rings that can be counted back from the present year to the year of scarring. The work by Parker and Jozsa (1973) is a good example of the use of tree-ring analyses to determine the time and frequency of severe floods and ice damage along northern rivers.

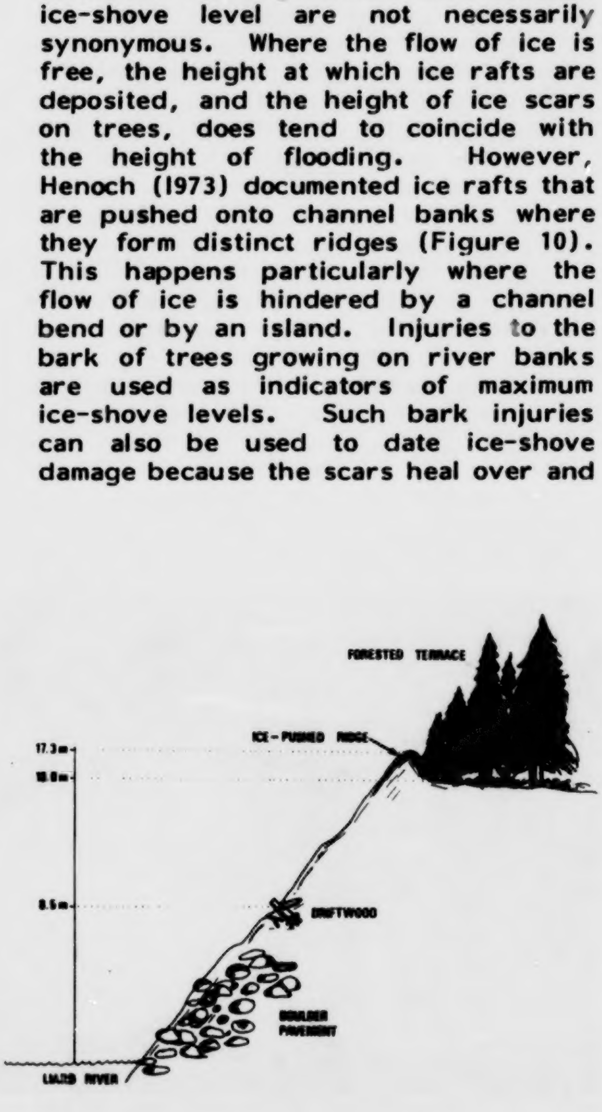

Figure 9. DRIFTWOOD, BOULDER PAVEMENT, AND AN ICE-PUSHED RIDGE ON BANK OF LIARD RIVER, 18 KM SOUTH OF FORT SIMPSON (adapted from Henoch 1973)

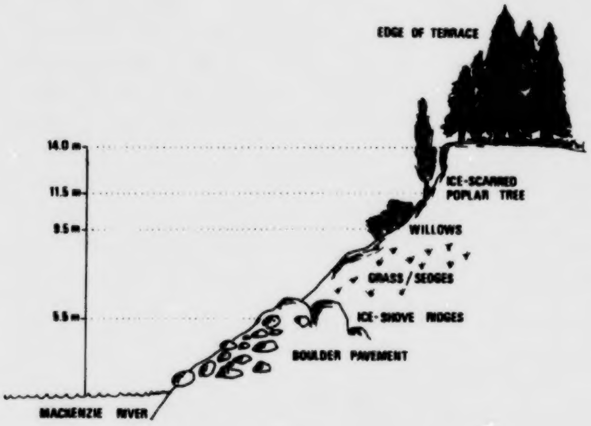

Figure 10. ICE-SCARRED POPLAR TREE AS AN INDICATOR OF MAXIMUM ICE SHOVE LEVELS, MACKENZIE RIVER OPPOSITE GREEN ISLAND (adapted from Henoch 1973)

c. Ice effects upon vegetation during flood periods: As documented along the Revillon Coupe channel in the Peace-Athabasca Delta (Doherty and LaRoi 1973), ice action during spring break-up is an important mechanical control over delta plant communities adjacent to channels. Ice shears off the tops of shrubs, as well as parts of rhizomatous plants, and removes large amounts of sediment from levee slopes. The plowing effect of ice also prepares the way for water erosion of the partially bared slopes during the ice-free season. The newly exposed areas may be re-occupied by downward expansion of upslope plant communities. If ice-shove has not been too severe, the newly buried zone may be occupied by a semi-aquatic community of horsetail, spike rush, rush and buttercup. However, if there is repeated ice scouring and water erosion the bank is undercut to form an unstable ledge that cannot support its vegetation. When the ledge and its vegetation fall into the channel, trees may be taken along and help to accumulate debris and sediment downstream.

In non-deltaic areas, regular scouring by ice is one of the forces that contributes to maintenance of vegetation in early successional stages along some reaches of channels. Sedge, cottongrass, and a variety of semi-aquatic grasses commonly grow in a band below the ice scour trim-line. Ice scour is responsible for maintenance of the trim-line (Figure 8) and without this regular event, woody species would invade some of the sedge and grass plant communities that provide a distinct habitat below the level of annual ice scour (Kellerhals and Gill 1973).

3. Summer Floods: In addition to possible inundation from break-up floods and snowmelt floods, both deltaic and non-deltaic areas of a river system may experience summer floods that result from heavy rainfall in other parts of the watershed. Another kind of summer flood can occur in outer portions of the Mackenzie Delta where storm surges sometimes move into the delta from the Beaufort Sea. Although not of major significance as a source of flooding, pile-ups of water in front of wind on Lake Athabasca can influence water levels on parts of the Peace-Athabasca Delta. Some features of the various types of summer floods are summarized below.

a. Summer floods in delta areas: Storm surges occur on the Beaufort Sea coast whenever strong northwesterly winds occur during the open-water season (Henry 1975). Sea level increases may reach 2 m and can flood huge areas of low-lying coastal lands and, in the case of the Mackenzie Delta, the current of the river may be reversed and the water may rise enough so that the effect is apparent as far as 140 km inland from the outer part of the delta (Stevens 1953). Siltation of lakes is greater in zones subject to storm surges than in the lakes above the level of such floods, because many of the outer delta lakes receive sediment-laden flood waters not only once each spring but also in summer as a result of storm-induced increases in water levels.

Historical analyses of past major storm surges indicate that the Mackenzie Delta was subjected to significant storm surges in 1905, 1929, 1944, and 1970 (Reimnitz and Maurer 1979). Although the 1970 surge height around the Mackenzie Delta was not recorded by Reimnitz and Maurer (1979), their analyses indicated that the 1970 surge height of up to 3.4 m above mean sea level on the Alaska coast was not equalled during the previous 100 years and may not have been exceeded in several hundred years. The storm on 17 September 1970 created a storm tide that took the life of two men who were sleeping in a hut on Tent Island near the mouth of the main channel entering Shallow Bay (Wilson 1971).

Recent mathematical modelling experiments have attempted to relate Mackenzie River outflow to storm surges (Henry and Heaps 1976). The model did not allow a simulation of the backing up of water and reduction of flow rate in the river as sea level increases, since the model was based on an assumed constant outflow from the Mackenzie River--an assumption that is physically unrealistic. The effect of river outflow on the storm surge has, however, been modelled. Henry and Heaps (1976) considered that the

Mackenzie River discharges through Shallow Bay, Reindeer Channel, Middle Channel, and East Channel in the proportions 3:6:5:6, but concluded that Shallow Bay is the only area where storm surges are amplified significantly by river outflow. Surge amplitudes in Kugmallit Bay are influenced very little by river outflow (Henry and Heaps 1976).

Many areas along the Beaufort Sea coastline, including the outer parts of the Mackenzie Delta, are subject to fairly rapid marine erosion. Storm surges greatly accelerate coastal erosion and at some points the retreat of shoreline during a major surge may be as much as 20 m, equivalent to several years of normal erosion (Henry and Heaps 1976). In the southern confines of Mackenzie Bay where outflow from the Mackenzie River has been demonstrated to increase surge heights, river discharge can be expected to be a contributing factor to storm-induced flooding and shoreline erosion. The dynamic balances between depositional and erosional processes, involving delta-building, erosion by storms, and redistribution of material by longshore currents, have not been defined in detail for outer portions of the Mackenzie Delta.

Even in the absence of storms, there may be widespread flooding of the Mackenzie Delta whenever high tides occur during periods of high water (Smith et al. 1964). The delta was almost completely under water three times in the years from 1948 to 1962. Floods and their timing can be a serious hazard to waterfowl and other delta wildlife. The inland extent to which brackish water is carried by such surges and the effects upon vegetation of possible inundation of brackish water have not been documented. The storm floods outlined in the section below for channel systems can also occur in channels within deltas following periods of exceptionally intense summer rainfall.

b. Summer floods in non-deltaic areas: Ice-jam floods and snowmelt floods are not the only source of high water levels for alluvial sites in the Mackenzie River Basin. Although spring snowmelt is considered to be the hydrologic event of greatest magnitude throughout the basin, recent research in the southern Mackenzie Mountains suggests that summer rainstorms are of particular hydrological significance (Brook and Ford 1980). Precipitation in the southern Mackenzie Mountains comes mostly in summer because in winter cold arctic air prevents movement of frontal low pressure systems into the area. As arctic air retreats northwards in spring, low pressure systems begin to follow more northerly paths. In summer, frontal lows from Siberia and the Bering Sea move southeastward over the Mackenzie Mountains and, combined with low pressure systems of Pacific origin, are the main sources of summer precipitation (Burns 1974). In the Nahanni area, 34% of the annual precipitation falls in July and August, the two months when low pressure systems are most frequent, and 69% occurs in the months of May, June, July, August, and September. It is possible, though, that the Nahanni area is not typical of all of the mountain watersheds within the Mackenzie River Basin because regular paths of low pressure systems converge west of Fort Simpson; low pressure air masses that move southeastward up the Mackenzie River valley and low pressure systems that move east from southern Yukon and down the South Nahanni River valley both result in summer precipitation in the Nahanni area.

It is also significant that summer storms are of such magnitude that they may influence hydrologic conditions for up to a year; Brook and Ford (1980) are of the opinion that a

July 1972 storm influenced runoff in the Nahanni area at least until June 1973, probably because freeze-up around 30 October had arrested drainage; as a result, spring meltwater was boosted by the release of arrested storm waters to induce a second flood within a span of 10 months. Expressed in general terms, such circumstances suggest that in many years, in mountainous parts of the Mackenzie River Basin, snowmelt may not be sufficient to cause prolonged flooding but may simply recharge groundwater that has been depleted by continuous flow of springs in winter. However, the spring snowmelt does saturate the soil and raise groundwater levels, leaving areas prone to flooding from intense summer rains.

An intense rainstorm in the Mackenzie Mountains from 19 to 21 July 1970 caused flooding and major changes to channel islands and bedforms in the Redstone, Keele, Mountain, and Arctic Red rivers, all west-side tributaries of the Mackenzie River (MacKay et al. 1973). That storm was unusual in its intensity; in some areas, small channel islands were entirely eroded and whole stands of trees were uprooted or flattened by the flood. In some parts of the floodplain, the vegetation mat was torn up rug-like and pushed aside by the moving water (Figure 11).

Figure 11. ALLUVIAL VEGETATION MAT CRUMPLED BY SUMMER FLOODWATERS ALONG TRIBUTARY OF MOUNTAIN RIVER, N.W.T. (Courtesy of S.C. Zoltai, Northern Forest Research Centre, Edmonton)

Tree-ring counts on trees that were broken off or flattened by the 1970 flood suggested a minimum occurrence interval of over 100 years since the last comparable flood. The probability of such a flood occurring in any given year might therefore be less than 1%. However, a low probability does not lessen the enormous ecological significance of such an event when it does occur. Henoch (1960) suggested that the storms that are relatively common in the Mackenzie Mountains in summer are orographic and convectional in origin; his observations indicate that some reaches of channels may respond to such rainstorms by rising as much as 6 m in a few hours. Storm floods in the relatively small drainage areas of west-side tributaries of the Mackenzie River can have a significant influence on water levels in the Mackenzie River itself. At Fort Good Hope, the Mackenzie River rose 2.9 m over the 20 to 23 July period in 1970, a unique event for the nine years of records preceding 1970.

Physical impacts from the 1970 storm that were visible on 1971 aerial photographs included: flood pathways cut through densely vegetated slip-off slopes, meanders and islands; erosion or complete removal of islands; construction of major new levees; and formation of new dune forms in braided sections of the flooded rivers. In Alaska, Viereck (1973) documented instances where storm floods induced deep thawing of ground ice.

MacKay et al. (1973) concluded that storm floods had the greatest physical impact on low portions of the active floodplain, with decreasing damage to cut banks, point bars, and channel islands. They concluded that storm floods are much more significant as a cause of floodplain changes on braided mountain streams than are snowmelt floods or break-up floods and accompanying ice-shove damages. Henoch (1973) also indicated that the heights of floods that occur during break-up on the South Nahanni River can be exceeded by the high floods that occur in summer during heavy rainstorms. However, the relative magnitudes of spring floodwaters and storm floodwaters will depend very much on each specific site; there are certain areas where ice jam flood levels exceed summer flood levels regularly.

In general, on a runoff basis, flood magnitudes of tributaries on the east side of the Mackenzie River are lower than they are for west-side tributaries. Basins on the east side of the Mackenzie River have a mean elevation that does not exceed 300 m above sea level, whereas west-side tributaries have basins with average mean elevations exceeding 750 m above sea level. This suggests a higher flood potential, constant adjustment of slopes and greater erosion and sedimentation in the west-side tributaries, in contrast to the more mature basin profiles of rivers on the east side of the Mackenzie River (Thakur and Lindeijer 1973).

b. Hydrologic Processes Important for Alluvial Vegetation and Wildlife during Non-flood Periods

The main processes of ecological importance during periods between floods are fluctuations of water levels, reversals of flow in delta channels, and complete freezing of water bodies. Some of the key features of these processes of non-flood periods are summarized below.

1. Fluctuations of Water Levels: Although flooding is emphasized in hydrological accounts of water levels, flood height alone is not the only feature of importance to plant and animal communities. Outflow or evaporation of floodwater, sometimes referred to as recession, is also thought to be ecologically important, although it is not well documented. It is known that timing of recession during the summer growing season is one factor that determines which plant species can establish themselves in exposed areas. Changes in flow regime that do not influence maximum flood levels but do influence duration of floods and rate of recession can have major effects upon plant and animal communities, as indicated by ecological events on the Peace-Athabasca Delta.

The key factors that contribute to lowered water levels are receding of floodwaters, evaporation, and lake outflow (Bennett and Card 1973). In winter, ice can have an influence on the magnitude of drawdown in lakes because if lake outlets freeze to the bottom, winter outflow can be arrested. The latter applies not only to delta lakes but also to large lakes such as Great Slave Lake and Lake Athabasca. Ice causes a major reduction in the outflow from Great Slave Lake and in some winters water levels of this lake actually rise as inflow exceeds outflow (R. Kellerhals, pers. comm. 1981).

Fluctuating water levels have a strong influence on species composition and structure of plant communities in the zone of inundation. In extreme cases, such as around hydroelectric reservoirs where the fluctuations may be frequent and of wide amplitude, the shoreline below maximum inundation level may be devoid of vegetation. Timing of the fluctuations is a factor of ecological importance because reservoirs associated with hydroelectric developments are often at high levels during much of the growing season. In less extreme cases, such as in alluvial sites that typify many of the channels in the Mackenzie River Basin, channel margins may display parallel vegetational zones that reflect different species tolerances to a given depth or duration of flooding and to burial by alluvium, not unlike the inter-tidal zone of coastal regions (Doherty and LaRoi 1973).

Areas subject to fluctuating water levels are dominated by plants that have special adaptations to meet such changing conditions. Perennial species that are able to live successfully in zones of intermittent immersion and repeated partial burial by alluvium generally have root systems that produce adventitous roots, such as in willow or spruce (Figure 12), or additional rhizomes, such as in horsetail or rush. Alternatively, annual plants such as bur-marigold or biennials such as marsh ragwort have life cycles that are timed to the annual periods of low water in places such as the Peace-Athabasca Delta (Doherty and LaRoi 1973).

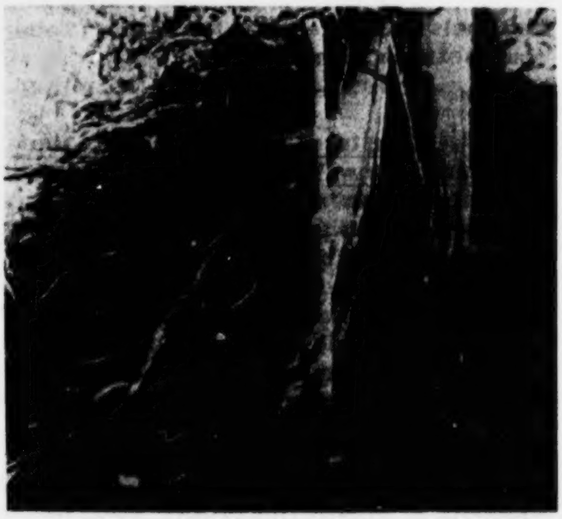

Figure 12. ADVENTITIOUS ROOTS ON STEM OF WHITE SPRUCE THAT WAS SUCCESSIVELY SURROUNDED BY ALLUVIAL SEDIMENTS DURING FLOODS (Courtesy of R.M. Strang, Forest Research Council, Richmond, B.C.)

2. Reversals of Flow in Delta Channels: Researchers who have documented relationships between water levels and plant community development along distributary channels in deltas have noted the effects of reversals of channel flow during summer. In the case of the Mackenzie Delta, flows into lakes during floods can create small deltas (Figure 13) in the lakes near the lake-channel junction and these geomorphic features create distinct habitats for vegetation development and waterfowl use (Gill 1973b). Reversing currents have also been documented from the Peace-Athabasca Delta where Doherty and LaRoi (1973) described plant community dynamics in areas where the spring floods of the Peace River reverses the flow direction of certain delta channels.

3. Complete Freezing of Water Bodies: Physical and biological processes in the Mackenzie River Basin are strongly influenced by freezing and thawing. Even in southern parts of the basin winter lasts about half the year, and in northern parts of the basin ground may be frozen for eight months each year. Most water bodies in the basin are entirely covered with ice during winter. Along the edge of the water body, there will be no free water and ground below the ice will also freeze. The area of a lake that freezes depends on temperature, depth of snow, depth of the lake and degree of mixing in the period before freeze-up.

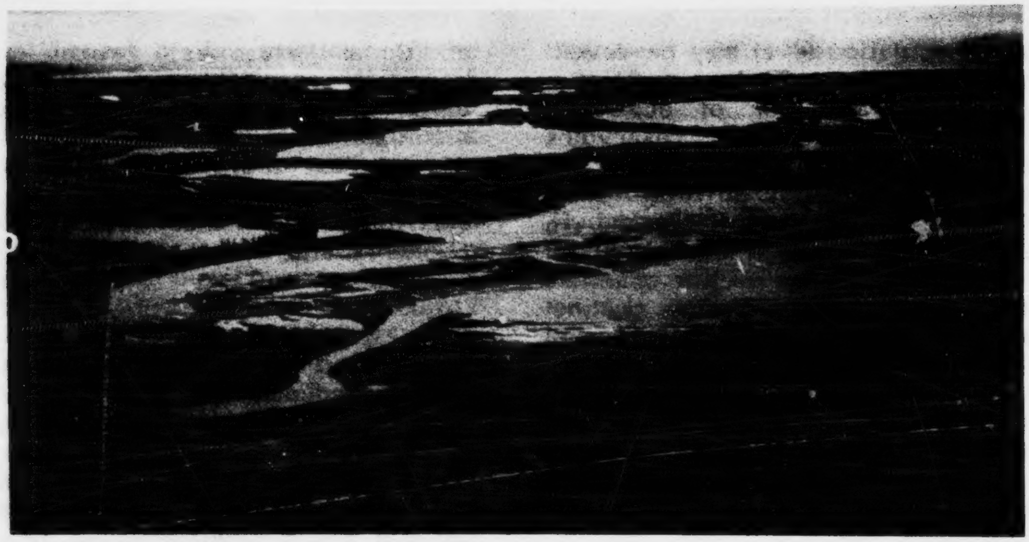

Figure 13. "REVERSE" DELTA BUILT INTO LAKE ON MACKENZIE DELTA (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

Rivers carry more water during fall than they do later in winter. After ice forms, water levels drop, leaving an ice cover hanging above water if the channel is very small. More commonly, however, the main part of the ice cover drops to the water level, except for a space under hanging shore ice.

In some parts of the major deltas, ice plays an important role in controlling drainage during winter. Lakes may be saved from being drained when their outlets freeze to the bottom, effectively damming further outflow. Even such large lakes as Claire and Mamawi on the Peace-Athabasca Delta appear to be controlled by ice blockages in drainage channels (Bennett and Card 1973). Such a feature has obvious implications for the entire biota of affected lakes. The level of Lake Athabasca is also influenced by ice. A massive ice sheet often forms in the shallow west end of the lake, with a resulting restriction of water outflow. Winter water levels at the west end of the lake in one year were up to 2 m lower than the main body of the lake. When such a phenomenon occurs, water levels in outflowing channels also recede to similar levels (Bennett and Card 1973).

4. Delta Hydrology under Regulated Flow: In deltaic areas, flow regulation can result in a variety of changes to sedimentary processes. For example, the minimum level of Lake Athabasca is controlled by a silt bar across the lake outlet, consisting of material deposited by spring floodwaters of the Peace River, during which the outlet channels reverse flow direction and carry silty water into Lake Athabasca. Regulation has reduced the occurrence of flow reversals and Kellerhals and Gill (1973) questioned whether this important silt bar, which represented an equilibrium between erosion and deposition, would remain. If the bar did not remain, water levels would be further reduced in Lake Athabasca.

CHAPTER III

CLIMATIC CONDITIONS DURING FLOOD PERIODS

The sections below provide a brief overview of climatic conditions during break-up and flood periods in spring and during summer storms. A separate section outlines the key mechanisms by which permafrost conditions interact with flood-related geomorphic processes.

A. Climate in Relation to Spring Break-up

In the Mackenzie River Basin some of the most important climatic factors influencing runoff are precipitation, temperature, and evaporation. Within the basin there are three broad hydrologic zones corresponding to three physiographic areas: Western Mountains; Interior Plains; and Canadian Shield. These three areas differ from each other significantly in terms of runoff.

The influence of precipitation on runoff is dependent upon seasonal distribution and intensity of precipitation. The Western Mountains and Interior Plains regions both exhibit pronounced maximum and minimum periods of precipitation whereas the Canadian Shield has a more even distribution. All three areas are subject to intense rainstorms that may produce high runoff. Summer rainstorms generally do not cause flooding unless they last for several days or unless there are several storms in rapid succession. The western Mountains region has a relatively high runoff due to orographic rainfall (Inland Waters Directorate 1973).

A key climatic feature of much of the Mackenzie River Basin is that temperatures are below 0° C for six months of the year, a circumstance that results in low runoff during winter. In spring, temperatures begin to rise in the south and west portions of the basin and the temperature rise progresses northeastward, producing a concurrent snowmelt progression. A sudden and prolonged rise in temperature during the snowmelt period can create severe flooding (Inland Waters Directorate 1973).

Most evaporation in the basin occurs between mid-April and mid-October when mean air temperatures are above 0° C. Evaporation is negligible during winter because of low temperatures, frozen surfaces, and a minimum of solar radiation. The amount of evaporation varies with the proportion of lake and pond area in the drainage basin, degree of imperviousness of surface, ruggedness of terrain, and channel density (Inland Waters Directorate 1973).

There are indications that climatic changes over long time periods may have an effect upon alluvial processes. A general cooling trend in the northern hemisphere between 1940 and 1967 resulted in an increase in precipitation and a decrease in evaporation, and consequently an increase in runoff. A comparison of the periods 1920 to 1940 and 1940 to 1967 showed an increase in runoff into the Arctic Ocean during the latter 27-year period (Antonov 1978).

Ice thickness is an important factor influencing the date of break-up and height of flooding in the Mackenzie Delta. For example, break-up occurred approximately 10 days later than average when ice thicknesses were greater than normal in 1972 (Anderson and MacKay 1973). Ice thickness is a function of temperature, snow cover, channel depth, and other factors. A gradient of declining mean annual temperature and decreasing snowfall exists within the Mackenzie Delta. Lowest temperatures and snowfall depths occur near the Beaufort Sea. Winds redistribute snow cover, and channels with thinner snow cover have a greater ice thickness than those where there is thick snow over the ice. In turn, channel size, channel orientation, and the type of vegetation cover on channel banks influence winds. A comparison of channel ice thicknesses indicates that north of Inuvik lesser amounts of snow, lower mean monthly temperatures, lower levee heights, and less vegetation cover combine to result in greater channel ice thicknesses than is the case in the portion of the delta south of Inuvik (Anderson and MacKay 1973).

In the Mackenzie Delta, prevailing winds have created several distinctive geomorphic features by influencing sediment deposition in delta lakes. Wave built shoals are found in lakes that receive large amounts of fine sediment or have shallow areas that are influenced by wave action. The building of shoals is a slow process as the amount of sediment deposited in any one year is minor. Shoals are only partly emergent, at most about 70 cm above the average summer water level, but may have a length of up to 1000 m. The edges of lakes that receive large amounts of sediment during spring floods often have horsetail communities on their edges. Such lake horsetail communities are similar to those found on positions of rapid sediment deposition along delta channels. The transporting ability of waves is lessened as waves reach the shallow shoreline and is further diminished by shoreline vegetation. For example, the outermost horsetail community in a delta lake studied by Gill (1971) received 4 cm of deposited sediment in 1967, whereas a sedge community a few meters closer to shore received half as much sediment.

The Mackenzie Delta is known to have warmer summer temperatures than the surrounding uplands, partly because weak low pressure systems periodically develop in the western Arctic in June, July, and August with the result that a wedge of warm air extends down the Mackenzie River valley from the south (Abrahamsson 1966). Gill (1971) suggested that the physical action of spring floodwater in lifting, breaking, and removing ice from the delta indirectly encourages a rapid increase in temperature. Nearly half of the delta is covered by lakes and channels, so the change in albedo caused by the flushing of ice by the spring flood can be significant. In addition to removing ice, the spring flood also inundates all but the highest levees on the delta. Consequently, high-albedo snow surfaces are flooded by silty water (Figure 14) and a relatively high amount of short-wave radiation is absorbed as soon as the flood waters subside. On areas adjacent to the delta where there is not the benefit of ice removal by flooding, lakes remain ice-covered for up to one month longer than nearby delta lakes. These circumstances allow white spruce and balsam poplar to grow on the Mackenzie Delta, creating one of the most northerly extensions of the boreal forest in North America (Kellerhals and Gill 1973).

B. Climate in Relation to Summer Storms

In dry periods of summer, most rainfall is lost to evaporation or is channelled into soil moisture and groundwater supplies. However, during conditions that lead to summer storms, excess runoff can produce high flood peaks. For example, Sellars (1973) documented a storm on 8 August 1972 in a small basin of the Mackenzie Mountain foothills in which the peak flow of the storm flood was as much as 36 times

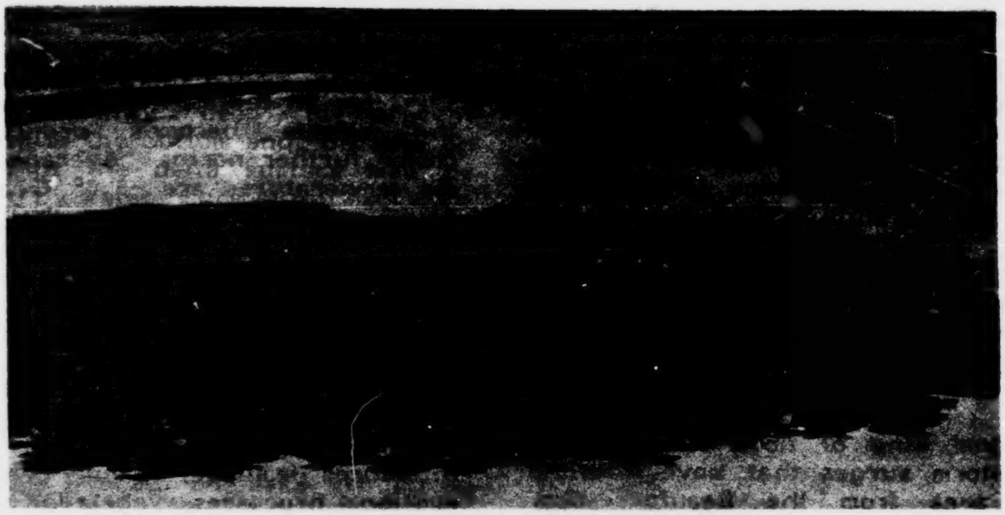

Figure 14. FLOODING OF SNOW AND ICE SURFACE BY FLOODWATERS IN SPRING, MACKENZIE DELTA (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

greater than the mean discharge. Conditions preceding the storm were such that little storm water went into storage; about 20 mm of rain had fallen in the two days before the storm and the main stream was flowing at twice its mean flow when the storm began. The storm that brought on the extreme storm flood lasted about 3 hr during which the total rainfall averaged through the small basin was 22 mm.

In the Peace and Liard river basins, during the time of river ice break-up, total precipitation is usually low in amount and river discharge at the time is primarily the result of snowmelt (Anderson et al. 1978). Break-up occurs during a period of rising flows. Flows generally continue to rise to a snowmelt peak that may occur within the period from late May to the early days of July. For the Liard River, almost all annual peak flows are due to snowmelt in mountains of headwater parts of the watershed; an exception occurred in 1974 when the annual peak occurred on 19 July and was caused by rain.

A severe flood with a calculated occurrence of once in 100 years was recorded in June 1972 at the town of Peace River, Alberta. Over a 35-hour period more than 15 cm of rain fell over parts of the Peace River basin southwest of Grande Prairie. Nearly simultaneous maximum flows of the Peace and Smoky rivers combined at the town of Peace River. To compare the magnitude of the June 1972 storm flood with the break-up flood of that year, flooding due to ice jams downstream from the Peace River townsite in April 1972 resulted in floodwaters that crested approximately 45 cm higher than the June flood (Warner and Thompson 1974).

The convergence of large, moist air masses over the watersheds of flooded rivers provides most of the precipitation for summer storms. In general, orographic precipitation is a significant portion of the total in mountainous areas (Warner and Thompson 1974). More localized orographic and convective precipitation results in relatively frequent floods in mountainous regions that have low storage capacity (MacKay et al. 1973). In the case of the June 1971 extreme flood of the Muskwa and Fort Nelson rivers, the main cause appeared to be heavy rainfall in basins with low storage capacity and which were already saturated with runoff from snowmelt (Smith 1975).

In the Mackenzie Delta, an additional kind of flood is associated with storm surges that move into the delta area from the Beaufort Sea. Storm-induced increases in sea level, referred to as storm surges, are common on the Beaufort Sea coast whenever strong northwesterly winds occur during the open-water season. These sea level increases commonly reach 1 m and sometimes 2 m, and may last for several hours (Henry 1975). There is some indication that, even in the absence of storms, there may be widespread flooding of the Mackenzie Delta whenever exceptionally high tides occur during periods of high water. The Mackenzie Delta was almost completely under water three times in the years from 1948 to 1962 (Smith et al. 1964).

A similar type of wind-induced flood is known for the Peace-Athabasca Delta where water may crest in front of wind at the west end of Lake Athabasca. On this inland delta, storm surges are not as dramatic as on the Mackenzie Delta. The consequence of a storm surge to the Mamawi-Claire part of the delta is to add water to the delta when the wind is from the northeast and to allow rapid drainage into Lake Athabasca when the wind is from the southwest (Card 1973).

C. Permafrost Interactions with Fluvial Processes

In the Mackenzie River Basin the climate becomes progressively cooler further north. Average annual air temperatures are -5.0° C at Sans Sault, -6.2° C at Norman Wells, and -10.1° C at Inuvik (Reid and Janz 1974, Kerfoot 1975). The thickness and occurrence of permafrost also increase as one progresses northward; for example, there is a permafrost thickness of 12 m at Hay River and 45 m at Norman Wells (Reid and Janz 1974). In the Mackenzie Delta, permafrost influences drainage, channel behaviour, erosional processes, vegetation growth, and a host of other characteristics of the delta surface (Kerfoot 1975). Examples of the influence of permafrost on characteristics of the delta surface are summarized below.

Most of the terrestrial portions of the Mackenzie Delta are underlain by perennially frozen ground. Permafrost thicknesses range from over 100 m in older parts of the delta to less than 30 m on the newest alluvial islands of the outer delta (Kerfoot 1975). In areas surrounding the modern delta, permafrost depths of 330 m have been found in the Caribou Hills. In the absence of the influence of water bodies, it has been estimated that the thickness of permafrost under mature spruce sites in the delta would be 170 m (Kerfoot 1975).

In terms of mean annual air temperature, the Mackenzie Delta is considered to be in the continuous permafrost zone, but within this zone there are significant areas that lack ground ice (Kerfoot 1975, Gill 1973). Where the depths of channels or lakes exceed the thickness of winter ice (up to 2.4 m), underlying sediments remain unfrozen because of the thermal influence of unfrozen pools (Mackay 1963). Most delta lakes and channels are sufficiently deep to prevent freezing to the bottom and, because up to 50% of the delta surface may be covered by water, much of the Mackenzie Delta is underlain by unfrozen ground (Gill 1973a).

The thawing effect of a water body is confined to an area immediately beneath the water body. The permafrost table around small delta lakes is known to plunge quite steeply at the lake edge. For example, temperature in the drill hole beneath one lake yielded no evidence of permafrost to a 70 m depth, whereas 10 m, 40 m, and 168 m away from the lake permafrost was encountered over the full depth of the holes (Kerfoot 1975).

Thermal modification of channels reflects the configuration and stability of the channel network. A stable channel has permafrost boundaries that plunge steeply downwards at the edge of the channel. As the channel migrates, so does the unfrozen ground although the lag in movement is greater with increasing depth. As the channel is replaced by an advancing slip-off slope, surface temperatures decrease and gradually the permafrost extends into the former channel bottom (Kerfoot 1975). In general, lateral migration of river channels results in thermal differences between the cutbank and slip-off slope and within the slip-off slope. Cutbanks at the outer bends of meanders are less affected by thermal changes resulting from channel migration than are the new initially unfrozen deposits of the slip-off slope, and permafrost thickness on the slip-off slope increases with distance from the river channel (Figure 15).

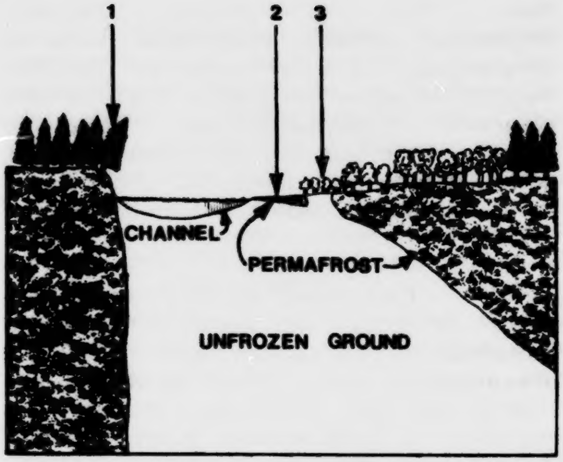

Figure 15. DISTRIBUTION OF PERMAFROST AND UNFROZEN GROUND ALONG AN ACTIVELY SHIFTING CHANNEL IN THE MACKENZIE DELTA

1. Cut bank; 2. Exposed horsetail zone where no snow accumulates and temperatures are low enough to induce permafrost; 3. Dense stand of Alaska willow where accumulated snow insulates soil sufficiently to prevent permafrost development (adapted from Smith 1975)

The overall effects of permafrost on river bank erosion have been described by Cooper and Hollingshead (1973), as summarized below. In regions of permafrost, river bank erosion appears to depend on the thermal regime within the river banks as well as on the properties of bank materials, the nature of bank and floodplain vegetation, and the severity of erosion. The presence of permafrost at shallow depths within a river bank tends to stabilize material that in an unfrozen condition would be inherently unstable and offer little resistance to hydraulic erosion. The effect of the thermal regime within the river bank is to make available on an annual basis an active layer that is easily erodible and in many cases with unstable slopes. The result is a rate of annual erosion that is relatively constant from year to year in comparison with the sporadic occurrence of bank erosion in rivers not affected by permafrost. Thickness of the active layer in a river bank depends on various factors including exposure, climatic conditions, river flow, the groundwater regime, vegetation cover, and bank material properties. A disturbance to the vegetation cover on a river bank or the adjacent floodplain can have a significant effect on thickness of the active layer and, hence, on the rate of bank erosion (Cooper and Hollingshead 1973).

Cutbanks in the Mackenzie Delta provide an example of the influence of permafrost upon erosional processes. Most delta cutbanks are nearly vertical. Frozen sediment is resistant to erosion and slumping, and the retrogression of a cutbank tends to occur at a pace comparable to the rate at which there is thawing of the bank face. A thawed layer forms parallel to the exposed face but, once a vertical bank is initiated, the presence of permanently frozen ground helps to perpetuate the vertical exposure. However, in some circumstances, as documented for the Colville River in Alaska, thermo-erosional niches can undercut river banks (Figure 16) and cause large blocks to break off (Walker and Arnborg 1963).

A typical sequence of erosional events, beginning in late May and early June before break-up flooding reaches a maximum, would involve thawing of faces of many cutbanks, particularly those facing south, where thawed layers may attain a depth of 0.5 m. Minor slumping and solifluction then begin, but the amount of material removed is relatively small. A thin veneer of thawed sediment may be removed by water when flooding begins, but this too is minor. There is less bank erosion than might be expected during the flood period. Because of the large amount of ice carried by channels during the spring flood, water temperatures remain just above freezing and therefore little water-induced thermal bank erosion can occur. In

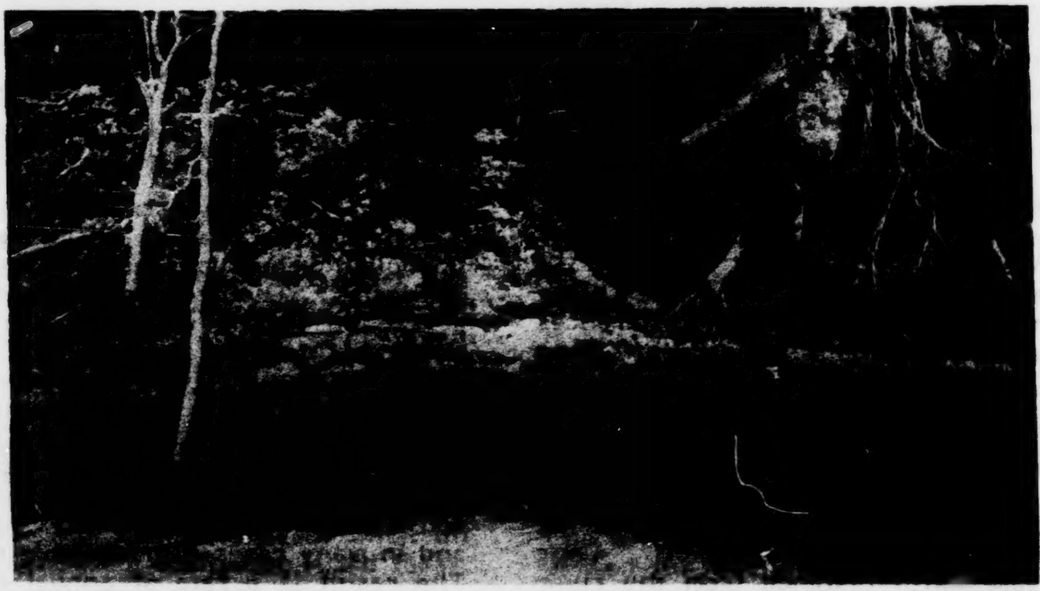

Figure 16. UNDERCUT RIVER BANK IN MACKENZIE DELTA (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

addition, the high level of the floodwater effectively blocks solar radiation and prevents thawing of sediment (Gill 1972a).

Ice is an important active erosional element in some locations of the Mackenzie Delta, especially where channels divide or along the outside bends of sharp channel curves. In some places, a band of ice may remain stationary against a cutbank while other ice moves down channel immediately against it. The stationary ice protects the cutbank and erosion is minimized. Frozen ground at the time of channel ice movement also helps to resist erosion from moving ice. After break-up, when flood levels subside and ice is no longer present, channel water temperatures rise sharply. Bank thawing then accelerates as a result of a greater heat exchange with warmer channel water; with reduced water levels the banks are also fully exposed to solar radiation. Slumping of south-facing cutbanks may remove large blocks of levee material. The rate of removal may be up to 3 m per year and has been observed to be relatively uniform from year to year (Gill 1972a).

As water levels fall in summer, a sequence of miniature shorelines is formed in the sediment of channel banks. Such features owe their existence to wind-induced wave erosion. The final process is bank recession caused by thermal and fluvial erosion of permafrost at the water line. Banks may be undercut by the thawing of material at the water line (Figure 16). Thawed material is rapidly removed by wave action which continues to expose the permafrost face to thermal erosion. With a combination of wind-induced waves and warm water, a wedge-shaped undercut may penetrate up to 5 m into frozen sediment in as little as 48 hours. As a result of such undercutting, large blocks of frozen sediment fall into the channel where they are removed within one or two weeks by thermal and fluvial erosion (Gill 1972a).

Complex interactions between vegetation, topography, and microclimate result in variations in permafrost distribution in the Mackenzie Delta. On a transect across a rapidly aggrading slip-off slope the following vegetation sequence was present: a sparse cover of horsetail nearest the channel; a dense growth of Alaska willow with an abundant understory of horsetail; a more sparse but taller growth of Alaska willow with a denser understory of horsetail and other plants; a willow alder zone with some mosses as ground cover; and mature white spruce with a dense understory of willow and alder plus moss ground cover (Smith 1975).

In summer, the different bands of vegetation possess distinct differences in ground temperature. The sparsely vegetated horsetail zone receives more sunlight on the soil surface than any other vegetation type, resulting in the warmest soil temperatures and deepest active layer. The surface layer of moss and organic matter in the willow-alder and white spruce zones insulates the subsurface, resulting in cooler soil temperatures. An experimental removal of 10 cm of organic material resulted in a 3° C increase in the mean daily temperature of the soil 10 cm below the surface (Smith 1975). However, variations in the amount of snow cover lead to ground temperature variations greater than those due to vegetation cover. Surface temperatures vary as much as 20° C under snow depths that range from 4 to 110 cm. At a depth of 1 m, soil temperatures can vary up to 6° C in midwinter over a horizontal distance of only 12 m; in summer the maximum soil temperature range at 1 m has been recorded to be as little as 2° C.

The lack of snow cover in the exposed horsetail zone results in winter heat losses so that the mean temperatures are low enough to induce permafrost. In contrast, accumulation of snow within the dense stands of Alaska willow insulates the soil sufficiently to prevent permafrost development (Figure 15). Snow blown off river channels in winter accumulates within the dense growth of Alaska willow (Figure 17). The drift pattern is related to the prevailing winds and is reproduced in a relatively consistent form each year. The extent of the permafrost-free zone is related to the extent of the snowbank itself. In general, snow cover is a factor that controls permafrost on the slip-off slopes adjacent to channels of the Mackenzie Delta (Smith 1975).

Another indirect link between climate and floods involves the influence of organic matter on equilibrium levels of the active layer. Development of permanently frozen ground is encouraged by build-up of organic material. On actively silting floodplains, regular deposition of sediment during floods prevents the growth of mosses and other ground cover that would encourage ground ice formation. In the absence of flooding and regular siltation, organic matter accumulation is no longer retarded, leading to increased moisture content of soils, reduced soil temperatures, and reduced active layer thickness (Kellerhals and Gill 1973).

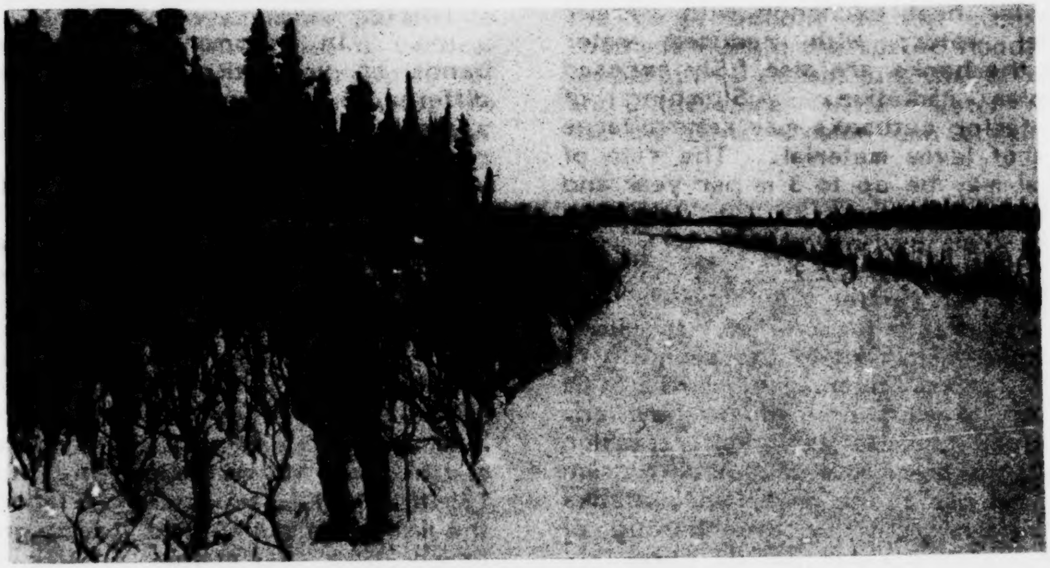

Figure 17. SNOW ACCUMULATION IN WILLOW ZONE OF POINT BAR ENVIRONMENT OF MACKENZIE DELTA (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

CHAPTER IV

THE LIFE AND DEATH OF ALLUVIAL LANDFORMS

Fluvial processes that control the build-up, maintenance, and destruction of landforms suitable for vegetational development are outlined in the sections below. Processes that influence vegetational development involve much more than the movement of sediments along channel systems and their deposition in deltas. Islands, channel bars, river banks, levees, floodplains, terraces, and lakes are all part of a complex balance between depositional and erosional processes. Background studies reviewed for the fluvial and geomorphic subjects of this chapter, but not summarized here, included: Axelsson 1967; Hickin and Nanson 1975; Ho and Walker 1976; Nemeth 1977; Nunnally 1967; Ritchie and Walker 1974; Smith 1979; Smith et al 1979; and Walker 1970.

A. Channel Systems

Channel classification systems proposed by Leopold and Wolman (1957) and by Rust (1978) were considered for use in this report, but the system suggested by Kellerhals et al. (1976) appeared to be more applicable to a discussion of ecological processes within alluvial sites of the Mackenzie River Basin. The latter system described channels according to three criteria: (1) channel pattern; (2) islands; and (3) channel bars and major bed forms. The different types of channels, islands, and bars are too complex to define here, but where descriptive terms are used they are based on definitions by Kellerhals et al. (1976).

Characteristics of an alluvial channel are established by variations in the discharge of water and sediment, as modified by the growth of vegetation along the stream bank. Maddock (1976) stressed that all changes in channel boundaries obey one simple rule: those changes that lead to equilibrium tend to persist and those that do not lead to equilibrium are destroyed. The characteristics that influence equilibrium are mean velocity, mean depth, mean width, mean sediment concentration, mean size distribution of transported sediment, and mean slope. However, because all of these characteristics vary, and because they are unique to given reaches of a channel, equilibrium is statistical, not absolute (Maddock 1976). In addition, certain streams tend to have distinctive characteristics; for example, tributary streams are usually anomalously wide near their confluence with a major river as a result of backwater conditions (Church 1977).

The configuration of a channel at any given time is not static and relationships between vegetational development and alluvial landforms are highly dependent upon the dynamic aspects of lateral channel migration. Kellerhals and co-workers used point bar deposits, meander scars, linear vegetation patterns, cut offs, oxbows, and former channel patterns on present floodplains to classify distinctly different types of lateral activity of river channels. Lateral changes in river channels are fundamentally important for the creation of new landforms that can be occupied by vegetation, and also for destruction of landforms and interruption of vegetational succession.

It has been shown that in northern environments, where river water temperatures remain substantially higher than mean annual ground temperatures, the transient effects of channel shifting may be traced for many decades in the ground thermal regime adjacent to the channel (Smith and Hwang 1973). In addition, the rapid erosion that may be associated with floodwater exposure of massive ground ice produces a chain of events important not only to engineering adjacent to northern rivers (Church 1977) but also to vegetational succession.

Along the Peace River, the one river of the Mackenzie River Basin now under regulated flow, certain changes to the channel system can be expected with time (Kellerhals and Gill 1973). In general, flow regulation has had the effect of reducing the size of the river without immediately changing the channel. The entrenched nature of the Peace River and the resistance offered by its bed materials prohibit significant changes in width, depth, or slope of the channel. However, deep scour holes at bends fill in during regulated flow and gravel bars exposed above the new high water mark become vegetated. For example, gravel bars on the Peace River that had been subject to active gravel transport were colonized by balsam poplar and willows up to 1 m tall after four years of flow regulation. Sections of steep and unvegetated river banks collapsed and were vegetated with willows. Such channel changes are important because if an exceptional flood should ever make spillage from the reservoir necessary then the reduced capacity of the downstream channel, as a result of filling of scour holes, bank collapse, and vegetational encroachment, will need to be taken into account (Kellerhals and Gill 1973).

Flood stages associated with snowmelt runoff are particularly significant for large rivers with gravel beds because flood periods are the only occasions when significant changes take place in the beds of such rivers; in general, large braided rivers with gravel beds are inactive from a morphological point of view and are unable to move most of their bed material until waters reach flood levels (Kellerhals and Gill 1973).

B. Sediments

Transportation of soil particles from the land surface to streams begins with the action of precipitation if it is great enough to cause surface flow of water. Soil sediments that are washed into streams by sheet erosion are usually grouped into two distinct categories: wash load, which never settles on the bottom of the channel because of stream turbulence; and bed load, which moves by rolling, sliding or hopping along the stream bed. Only limited information is available for bed load movement in Canadian rivers, so published maps generally show only suspended sediment concentrations, including wash load which is very fine material with a low settling velocity in still water (Fisheries and Environment Canada 1978). The latter category is significant in some parts of the Mackenzie River Basin; for example, suspended material in the Peace River is almost entirely wash load (Kellerhals and Gill 1973).

The sediment yields of the Mackenzie, Athabasca, Slave, and Liard rivers are examples of naturally high suspended-sediment loads (Fisheries and Environment Canada 1978), especially when contrasted with rivers such as the Great Bear River. However, in comparison with most other large rivers of the world, the northern rivers of Canada have relatively low sediment loads. Sediment loads are closely related to the amount of natural storage in a basin and rivers with little storage, such as the Peace River, have suspended sediment loads that vary from negligible values in winter to as high as 2 000 mg/L during floods (Kellerhals and Gill 1973). This range is relatively low by most standards. In late June and July, as a result of severe storms, sediment discharge on the Fort Nelson and Muskwa rivers has been observed to increase sharply and in 1979 peak sediment concentrations in early July greatly exceeded those observed in spring on these rivers.

Sediment load in the Mackenzie River, for all practical purposes, is significant only downstream from its main tributary, the Liard River. Just as the Fort Nelson River yields a large amount of sediment to the Liard River, the Liard has the same role in relation to the Mackenzie River (Grey and Sherstone 1980). The Mackenzie River transports little suspended matter where it issues from Great Slave Lake, and even where it is joined by the Liard, 330 km downstream from Great Slave Lake, Mackenzie River water has picked up little sediment en route. In contrast, the Liard River enters the Mackenzie as a silty, driftwood-laden river. The sheer size of the Mackenzie River results in a considerable downstream stretch where Mackenzie and Liard waters do not mix (Mackay 1970).

Whatever role suspended sediments and water quality have upon the development of alluvial sites, the effects are not necessarily equally applicable to both sides of a channel downstream from the mouth of a tributary that is contributing a sediment load to the system. For example, Mackay (1970) showed that in early June 1968 warm, turbid Liard River water did not mix fully with the cold, clear Mackenzie River water for a distance of about 480 km downstream from the confluence of the two rivers at Fort Simpson. This means that, downstream from Fort Simpson for a considerable distance, west bank alluvial sites would be in contact with turbid Liard River water and east bank sites would be in contact with clear Mackenzie River water. Incomplete mixing has also been demonstrated by temperature profiles in the Mackenzie Basin downstream from the confluence of the Great Bear River; the influence of relatively cold water from the Great Bear River was noticeable for up to 500 km downstream (Mackay 1972).

In general, sizes of particles and flood water velocities and depths are the main factors that influence original deposition of suspended sediment loads; subsequent re-distributions are caused mainly by wind and wave action. Sediment load also influences meander migration across alluvial plains by building onto the inside bank, through point-bar construction from bed load, and by raising the elevation of point bars to floodplain level through suspended load deposition in the emerging successional vegetation. A reduction in sediment load has the effect of widening channels at meander bends (Kellerhals and Gill 1973).

The quality and quantity of suspended sediment load can have a direct influence on survival and distribution of certain plant species in delta areas. Doherty and La Roi (1973) noted that submerged plants were absent where light penetration was limited by the large and fluctuating suspended sediment loads of the Revillon Coupe channel in the Peace-Athabasca Delta, but such vegetation was present in nearby waters of Lake Athabasca marshes where turbidity was lower. In turn, established vegetation can have an influence on how sediments are deposited. For example, in the Peace-Athabasca Delta during the 1971 flood season, groups of reeds (**Phragmites communis**) had about 2 cm of sediment accumulated around the edge of each clump but negligible amounts deposited in the centre of each clump (Doherty and LaRoi 1973).

Inter-relationships between sedimentation and vegetational development have been used in studies of depositional and erosional processes in flood-prone areas of the Mackenzie River Basin, including tree-ring dating of floodplain vegetation to estimate rates of river channel shifting over periods of several hundred years (Hickin and Nanson 1975), use of willow ages to estimate minimum periods of river bar stability (Church 1977), and examination of adventitious roots (Figure 18) to study rates of sediment addition to floodplains (Wagg 1964, Strang 1973). In studies outside of the Mackenzie River Basin it has been demonstrated that the form of tree bases can be influenced by the timing of sediment deposition. A flared base, with the widest part at the base and now buried by sediment, indicates recent deposition; an inverted cone-shaped base (Figure 19) suggests early and repeated deposition of sediment (Sigafoos (1964).

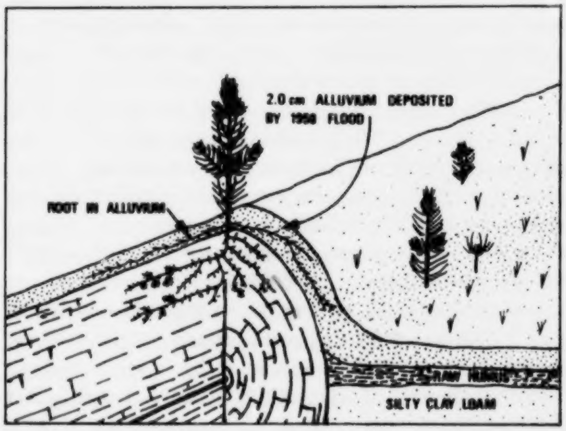

Figure 18. ADVENTITIOUS ROOT DEVELOPMENT IN THREE-YEAR-OLD WHITE SPRUCE SEEDLING AFTER ALLUVIUM WAS DEPOSITED OVER DECAYED WOOD ON WHICH THE SEEDLING HAD ORIGINALLY GERMINATED, SLAVE RIVER LOWLANDS (adapted from Wagg 1964)

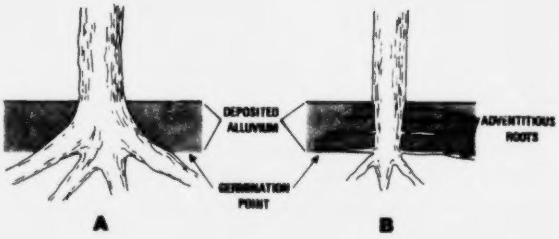

Figure 19. VARIATION IN FORM OF TREE BASES IN RELATION TO RATE OF DEPOSITION
A. flared base suggests recent deposition;
B. inverted cone-shaped base with adventitious roots suggests early and repeated deposition (adapted from Sigafoos 1964)

C. The Battle Between Depositional and Erosional Processes

Depositional and erosional processes are complex in flood-prone areas and so are the scientific terms that are used to describe these processes. Therefore, to interpret relationships between vegetation development and depositional or erosional processes in alluvial sites, it appeared to be most meaningful to restrict this review to alluvial landforms that generally met two criteria:

- the types of alluvial landforms selected for discussion were subdivisions of the landscape that were thought to have conspicuous relationships with vegetation patterns;
- the different alluvial landforms recognized were based, wherever

possible, on processes (such as deposition or erosion) rather than on appearance (morphology).

Vegetation plays an important role in the deposition of alluvial landforms, particularly the reaction time associated with variations in the discharges of water and sediment. In the absence of major floods, vegetation continually encroaches on the stream channel, increasing bank resistance and reducing the rate of change of bank position (Maddock 1976). Such effects are negligible in large rivers of the Mackenzie River Basin. In small tributaries, however, vegetation can be expected to have significant influences through encroachment (Kellerhals and Gill 1973), with well-vegetated channels tending to be narrower than those without vegetation. If a channel loses its fringe of vegetation cover, the unprotected channel will become wider than the original. When trees are removed by major floods they provide another interaction with geomorphic processes downstream where floating trees may be part of the debris responsible for jams, localized flooding, and channel diversions.

The balance between depositional and erosional processes is of fundamental importance to plant succession and primary productivity of alluvial sites. Along rivers, plant succession is usually initiated on new ground formed by deposition of sediment during floods (Figure 20). Since valleys do not provide space for unlimited lateral expansion of new deposits, to have new space for alluvium to be deposited there must be periodic destruction of older sections of the floodplain (Kellerhals and Gill 1973). Destruction of older soil-vegetation complexes and redistribution of their nutrients into newly exposed alluvial deposits is thought to be one of the reasons that floodplains have a relatively high primary productivity. Without continued initiation of primary succession by the physical forces of floodwaters, the biological productivity of northern floodplains and deltas would diminish.

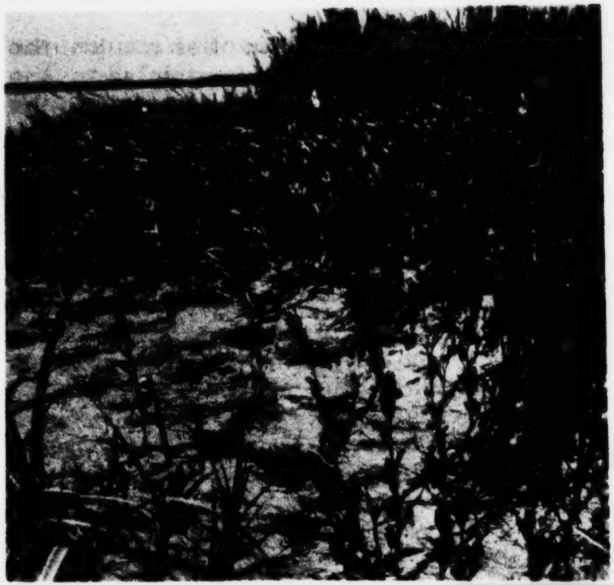

Figure 20. INITIATION OF PLANT SUCCESSION ON NEW GROUND FORMED BY DEPOSITION OF SEDIMENTS DURING FLOODS, SLAVE DELTA (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

D. Islands and Channel Bars

Where the terms, bars and islands, are used in this report, bars include those landforms that are submerged at bankfull stage, whereas islands are normally emergent at bankfull stage. Bars tend to be non-vegetated, except for point bars which are associated with more permanent parts of channel systems; islands are normally vegetated.

In general, where bars are a component of the alluvial sites discussed in this report, they refer to the relatively stable parts of a channel system; point bars at the bends of rivers fall into this category. Point bars are stable enough to allow vegetational development because the bar's existence depends mainly on the long-term position and shape of the channel. The dynamic sequence by which point bars, and associated meander depressions, are formed along migrating channels is portrayed in Figure 21.

The large variety of bar forms that are influenced mainly by short-term variations in flow and sediment supply (Smith 1978) were considered to be of little importance to the ecological processes summarized in this report. The information presented here refers to bars that are relatively permanent parts of the channel system but ignores those that are highly mobile and unstable. The parts of the biophysical system that are the most stable, such as islands, levees, terraces, floodplains, and deltas are given the most attention in subsequent discussions of ecological processes in alluvial sites.

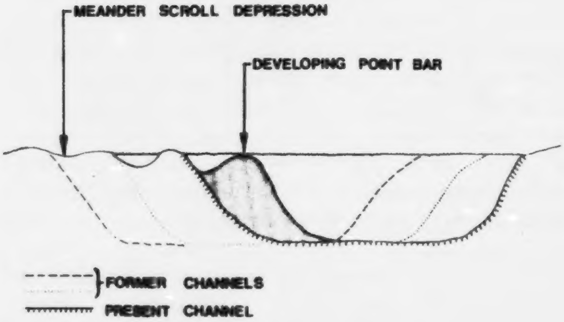

Figure 21. POINT BAR FORMATION IN A LATERALLY MIGRATING CHANNEL (adapted from Hickin 1974)

E. Levees and Floodplains

Within the Mackenzie River Basin, levees are a prominent landform mainly within deltaic portions of the basin. Levees are of particular ecological significance because, hydrologically, they represent the maximum heights of floodplains. On the Mackenzie Delta, estimated heights of levees above late summer low water levels are 1.5 m near the outer edge of Richards Island, 3.0 m between Tununuk and the south end of Shallow Bay, 6.0 m between Inuvik and Aklavik, and 9.0 m near the southern end of the Mackenzie Delta. The older and higher floodplains found in the southern half of the delta have poorly developed levees. In the southern part of the delta, channel banks are covered mainly by spruce forest; although such areas may be flooded occasionally, little sediment is deposited. In contrast, levees are much more abundant in the northern half of the delta, where levees tend to be close to the channel, usually within 15 m of the low water edge of the channel. The levee crest is usually only one or two meters wide (Mackay 1974).

In general, levee construction tends to keep pace with bank recession (Mackay 1974). The amount of sediment deposited along the backslope of aggrading levees is in equilibrium with the rate of recession along bank faces, with the result that levees migrate across delta floodplains; this type of levee has been designated as a "cut-bank levee". Young levees rapidly aggrade due to sediment accumulation during floods; such levees annually receive as much as 10 cm of alluvium (Gill 1972a).

Within the Mackenzie Delta, ice abrasion, slumping, solifluction, and fluvial erosion are the erosional agents that modify levee morphology, but wave action and melting of previously frozen sediments are also significant in the alteration of levee forms. Most of the destruction of cut-bank levees is accompanied by deposition along their backslopes; thus, this type of levee is seldom totally removed by erosion. In much of the Mackenzie Delta, cut-bank levees are in dynamic equilibrium between the opposing forces of erosion and deposition (Gill 1972a).

Levees also play a dominant role in the Peace-Athabasca Delta which is a typical "bird's-foot delta". The growth of the bird's-foot pattern is mainly the result of a build up of levees along distributaries to a height above the average water level during floods. The distributaries commonly split and then re-unite to enclose depressions between them; such depressions become deltaic lakes and marshes (Bayrock and Root 1973).

During floods, water in distributaries overflows the channel banks, sand is deposited on levees, and silt and clay become trapped in intervening lakes or marshes. Delta lakes often receive sediments through levee breaches; miniature deltas usually develop at such breaches and extend into delta lakes. Breaches in levees may also serve as drainage channels for lakes when the flood stage is receding. Thus, a delta lake may be flooded or drained by the same levee breach. Once a breach develops in a levee, sedimentation is accelerated in nearby delta lakes. However, levee breaches tend to be filled with silt relatively quickly, thereby re-sealing the nearby delta lakes (Bayrock and Root 1973).

Floodplains have distinct characteristics that influence drainage which, in turn, has a strong influence over vegetational development. Ground tends to slope downwards with increasing distance from stream channels on floodplains. In addition, natural levees contain materials that are more coarse than those deposited some distance from the streams. Old levee deposits may interfere with drainage and much of the floodplain area may be poorly drained. Tributaries also complicate floodplains. Like the main stream, tributaries also change positions and have their own levees. These levees may be high enough to block the normal flow of water over a floodplain, with resulting drainage problems and vegetation changes near the mouths of tributary streams.

F. Deltas and Delta Lakes

In the case of the Peace-Athabasca Delta, three subdivisions can be recognized according to prevailing physical deltaic processes: the active, semi-active, and inactive portions of the delta (Bayrock and Root 1973, Dirschl 1973). The active delta consists of flowing rivers and their deposits such as point bars, levees, and very gently sloping delta plains surrounding open basin lakes. The active delta is directly affected by hydrologic events such as ice-jam floods, the later snowmelt flood or high water levels on Lake Athabasca.

The semi-active delta includes perched basins and cut-off stream channels, which are not connected with the major hydrologic system but are generally recharged by floodwaters in spring (Figure 22). The inactive delta consists of closed basins, old meander scrolls, and swamp areas that are positioned on the higher, older portions of the delta and are affected by the floods only during extreme high-water years. Active delta locations that receive deposits of alluvium also receive nutrients required by plants. In contrast, waters that reach semi-active and inactive delta locations have already

Figure 22. SEMI-ACTIVE PART OF A DELTA WITH A LOG-FILLED CUT-OFF CHANNEL THAT IS ACTIVE ONLY DURING HIGH FLOODS (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

deposited their sediment load and nutrients on active delta locations. As a result, total nutrients tend to be higher, on a sustained basis, in active delta locations than in semi-active or inactive portions of the delta.

There is a great variety of lake forms on deltas. For the Mackenzie Delta, five broad types of lakes have been recognized: abandoned channel lakes; point bar lakes; floodplain lakes; thermokarst lakes; and dammed lakes (Mackay 1974). It is commonly assumed that all delta lakes are relatively productive for the growth of aquatic vegetation, but Mackenzie Delta studies revealed distinct differences in productivity of various lakes (Gill 1973b). Thermokarst lakes are always above the normal summer channel water level and are therefore only rarely flooded. They occur in the upper, older parts of the delta where there is normally a flood around the second week in June and a subsequent lowering of water levels throughout the year. Because thermokarst lakes are not connected to delta channels, they are insulated from the sharp changes in water level associated with regular flooding and recession. The water level in these lakes is relatively high all year, with only a rise of about 15 cm during the spring runoff period. In the Mackenzie Delta, approximately one third of the lakes are of the thermokarst type. They are bounded by small ridges so that they receive an input of nutrients through sediment transport only during particularly high floods. Most thermokarst lakes are also subject to bank erosion as a result of melting of ice-rich materials; the bank instability prevents development of littoral plant communities, a circumstance that adds to the relatively low vegetational productivity of the lakes. The ridges around thermokarst lakes are often covered with spruce trees that extend to the edges of the steep lake banks (Figure 23).

By contrast, another third of the lakes of the Mackenzie Delta are floodplain lakes that are connected to small channels. Such lakes receive nutrient-rich sediments during flood stage (Gill 1973b). Floodplain lakes closely follow the water level regime of connecting delta channels; the latter function as inlets to small lakes during flood stage and outlets after flood stage. Channels may reverse flow direction at any time during summer when water levels rise or fall, for example during storm floods, but usually they provide one major input to a lake during high water in spring. It is at the flood stage that floodplain lakes receive organic debris, ice and nutrient-laden sediments. Wherever small channels enter floodplain lakes there are delta-shaped deposits of alluvium formed. Some lakes of the delta are filling in rapidly as a result of the annual alluvial deposits and, when

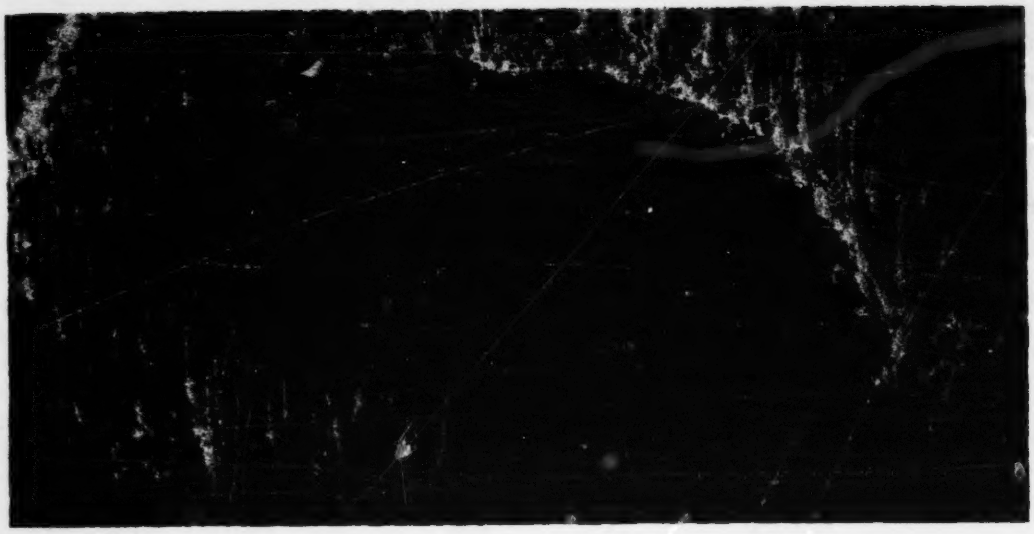

Figure 23. THERMOKARST LAKE IN MACKENZIE DELTA (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

filling is well advanced, shoals are developed within the lakes by wave action; such processes are evident along the channel that joins the south end of Campbell Lake to East Channel.

On the Peace-Athabasca Delta, small lakes and basins are unaffected by permafrost. The delta is in an area of discontinuous permafrost, but is warmer than surrounding areas and virtually permafrost-free (Bayrock and Root 1973). As a result, the Peace-Athabasca Delta lacks thermokarst lakes that typify portions of the Mackenzie Delta. There are three main types of basins on the Peace-Athabasca Delta: basins with an unrestricted hydraulic connection with a large lake or river channel, the level of which increases or decreases with lake or channel level; basins with a restricted connection with another lake or river channel in which water levels may have a direct relationship to levels of a nearby large water body at high water levels but no connection at low water levels; and perched basins with no inlet or outlet channel (Bennett and Card 1973). Occasionally perched lakes and restricted drainages gain water from wind-generated rises in water level (Card 1973), but floodwaters in spring are the main source of recharge.

On a geological time scale, inland deltas such as the Peace-Athabasca and the Slave are relatively short-lived landscape features. Eventually sediments fill the depressions in which such inland deltas develop and rivers then flow through the deltas without deposition. Actively growing deltas are dynamic landscape features. Position and size of individual distributaries may change often, but the greatest changes occur when the area of deposition shifts from one part of a delta to another. In all deltas, the part of the delta that is actively growing periodically migrates. Distributary channels become over-extended and are later abandoned in favour of a shorter, steeper gradient to the main body of water. For example, the distributary system of the Athabasca Delta is overextended to the east and migration of the largest distributaries, probably into lakes Claire or Mamawi, was considered to be imminent in 1972 (Bayrock and Root 1973). Overtension of the distributary system can now be considered to be artificially maintained as a result of dredging along the eastern channel (R. Kellerhals, pers. comm. 1981).

CHAPTER V

VEGETATION IN ALLUVIAL AREAS

Plant successional trends on deltas and on non-deltaic alluvial sites are summarized from previous studies within the Mackenzie River Basin. Vegetational succession was considered to be so strongly influenced by the distinctive combination of climatic, edaphic, and other physical features of a site, and also by the availability of plant populations capable of occupying any given successional stage, that descriptions of successional sequences from study areas outside of the basin were judged to be of only limited use for the summary presented here. Some information is included here from studies along the Chena River in Alaska (Viereck 1970) and the Saskatchewan River Delta (Dirschl 1972, Dirschl and Coupland 1972). Other reports reviewed for information on successional relationships of alluvial sites included: Bliss and Cantlon 1957, Johnson and Vogel 1966, and Viereck 1966 for Alaska; Chalidze 1973, Gorchakovskii and Peshkova 1970, Hamet-Ahti 1970, and Remezova and Vostokova 1978 for the Soviet Union; and Dahlskog 1966 for a mountain delta in Swedish Lapland. However, none of the latter Alaskan, Russian or Scandinavian reports were summarized for this chapter; they were simply reviewed as background material to provide insights into relationships between vegetation and fluvial processes in northern alluvial ecosystems.

The Mackenzie River basin is a large area within which variations in climate, plant distribution, soil types and other factors result in a relatively great range of vegetation types. For example, seventeen different forest sections (Rowe 1972) occur within the basin. Such complexity could not be easily compressed into this review, with the result that vegetational information has been selectively chosen to bring out features common to many of the alluvial sites within the basin. More detailed analyses would be required to document all the variations that exist between vegetation and fluvial processes within the basin.

Productivity of vegetation on alluvial sites is analysed from data derived from studies within the basin, supplemented with data from several other studies outside of the basin where specific comparative productivity data were available in relation to severity or frequency of flooding.

It should be emphasized that the review presented here is very much influenced by the locations for which data are available, generally the sites where the most detailed studies have been done. For example, within the basin there have been relatively detailed studies of alluvial ecosystems at locations such as the Mackenzie Delta, the Peace-Athabasca Delta and the Beatton River and references for such locations are frequently cited. In contrast, there has been relatively little documentation of ecological processes on alluvial sites in places such as the Lower Peace River in British Columbia, along the Athabasca River below Fort McMurray, or on the Slave Delta. Because emphasis was placed upon information from sites where the most detailed information was available, it is necessary to be cautious about extending to all portions of the basin the successional sequences summarized for the documented sites. As a specific example, accounts of ecological processes along the Beatton River (Nanson and Beach 1977) are cited frequently, although the geomorphic structure of the Beatton River is representative of only a few reaches of channel within the Mackenzie River Basin. The reader should not indiscriminately apply the Beatton River data to other alluvial sites along all tributary channels within the basin.

The vegetation of islands is not reviewed separately here. In many cases, successional sequences on islands can be considered to be similar to those documented for non-island alluvial sites, except that islands tend to be especially protected from the forest fires that sometimes sweep across vast areas of boreal vegetation. The broad relationships between frequency of flooding and vegetation type, as outlined in the sections below, generally apply to islands. For example, portions of islands that regularly receive new quantities of sediments from flooding will tend to be dominated by willow and horsetail communities similar to those documented for point bars; portions of islands that are well drained and infrequently flooded will usually support stands of balsam poplar or white spruce, similar to the plant communities on the upper parts of levees along channels. The edges of some islands are subjected to ice scour with a grassy type of vegetation in the zone of scour similar to that which typifies ice-scour zones along other channel margins.

A. Plant Succession on Deltaic Alluvial Sites

To simplify the variety of successional sequences that occur on the diverse deltaic landforms of the Mackenzie River Basin, successional trends of the Peace-Athabasca Delta (Dirschl 1973) have been taken for a sample description of geomorphic processes and vegetational development on deltas within the basin. In the Mackenzie Delta, the presence of permafrost and its effects on geomorphic processes, as well as the effects of the Beaufort Sea on the outermost portions of the delta (Gill 1971, Kerfoot 1975, Reid and Calder 1977), would result in some variations from conditions described for the Peace-Athabasca Delta.

Plant communities recognized in the successional series of the Peace-Athabasca Delta were grouped into five types: aquatic communities in open water; shore communities and mudflats, including emergent vegetation; meadow communities; shrub communities; and forest communities, both deciduous and coniferous. Vegetation succession patterns vary in different parts of the delta. Within active and semi-active locations, aquatic and emergent communities are replaced by various shoreline pioneers on emerging mudflats which later develop into meadows. Meadows are first replaced by willow shrub communities and eventually by forest communities (Dirschl 1973).

Succession on the Peace-Athabasca Delta does not follow a single pathway but takes the form of a branching network in which several distinctively different species or species groups may dominate apparently identical sites during some specific successional stage, and then all give way to a single plant community at some succeeding stage. In the Peace-Athabasca Delta the variety of alternate dominance types was particularly great among shoreline and meadow communities. It is not clear why sites that appear to be physically and successionally identical are occupied by different species groups; the supply of plant seeds at the time when conditions are favourable for germination and minute local differences in moisture and nutrient status are probably involved in creating such differences (Dirschl 1973).

Several of the vegetation communities and successional sequences described in the Mackenzie and Peace-

Athabasca deltas are very similar. For example, on levees in the Peace-Athabasca Delta, a common sequence is horsetail, willow, alder, balsam poplar and finally white spruce on succeedingly higher and older portions of levees (Doherty and LaRoi 1973). On well defined levees in the Mackenzie Delta, the same sequence exists (Gill 1972a, Reid and Calder 1977), although the species of horsetail, willow and alder differ from those in the Peace-Athabasca Delta. Another difference is that white spruce (Figure 24) is not present in all parts of the Mackenzie Delta; spruce is restricted to levees at least 3 m above the normal summer water level or sea level (Gill 1972a, Kerfoot 1975). Where the delta is younger, as in the outermost portions, levees are less than 3 m and therefore white spruce is not found. In portions of the outer Mackenzie Delta where white spruce and balsam poplar are not found, a progression of horsetail, willow and alder was observed on the highest and best defined levees (Reid and Calder 1977).

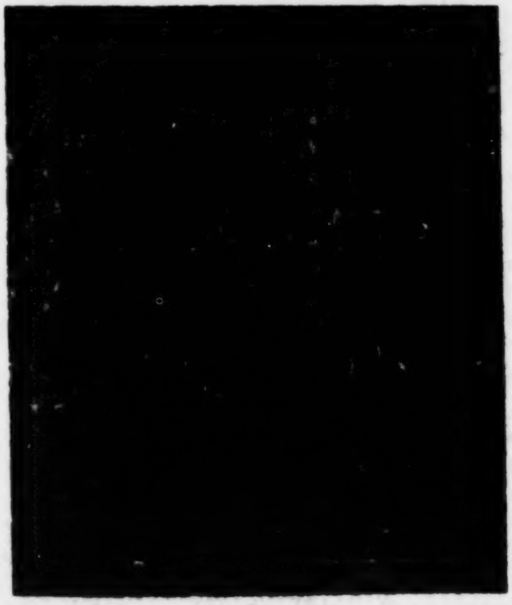

Figure 24. MATURE WHITE SPRUCE ON UPPER LEVEE ALONG CHANNEL IN MACKENZIE DELTA (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

Large areas of poorly drained meadows are common to the Peace-Athabasca and Mackenzie deltas (Dirschl 1973, Reid and Calder 1977). A variety of sedges, grasses and rushes dominate such meadows. The wet meadows are periodically inundated by standing or slowly moving water. Surface water is seasonal but the water table remains in the rooting zone of plants during at least part of the growing season. Meadow areas have a flat topography and therefore large areas can be flooded with water level increases of as little as 0.5 m. Such meadows are flooded by waters that have already deposited most of their sediment in active delta locations or by water from local runoff which carries little sediment. As a result, the rate of sediment deposition on meadows is very slow compared to that on levees and point bars.

The relatively slower sediment accumulation in meadow areas of deltas means that increases in depth of soil above the water table are also relatively slow, as is the succession to vegetation types that require drier soil conditions. Illustrative of the relative stability of meadows in the Peace-Athabasca Delta is an area south of Mamawi Lake that was mapped as meadows dominated by slough sedge in 1930; when mapped again in 1971 the same area was dominated by reed bentgrass meadows and low willow shrubs (Dirschl 1973). Soil conditions had become only slightly drier over a 41-year period, and some of this change was probably a result of general drying of the delta in the three years immediately following closure of the W.A.C. Bennett Dam in 1968.

Older portions of both the Peace-Athabasca and Mackenzie deltas are infrequently disturbed by hydrologic events. Succession in these inactive delta locations is controlled predominantly by autogenic processes. The lack of a source of nutrient-rich waters in older parts of the deltas results in a gradual build-up of available nutrients in the form of humus and other undecomposed organic matter, the growth of floating sedge mats over depressions, and finally the filling of entire depressions with muck and peat. In the process, peat surfaces eventually grow completely out of reach of the water table. Once the peat surface is high enough to be invaded by **Sphagnum** mosses, it develops into a nutrient-poor bog or muskeg. A relationship between frequency of flooding and amount of bog development on deltas is implied by the fact that extensive bogs are present in the Saskatchewan River Delta where major floods were historically less frequent than in the Peace-Athabasca Delta (Dirschl 1972). In the Peace-Athabasca Delta, only the oldest portions of the delta contain floating sedge mats. Frequent high floods are believed to be responsible for the majority of the Peace-Athabasca Delta remaining at early successional stages (Dirschl 1973). As outlined in a later chapter of this report, periodic flooding of plant communities and maintenance of a significant portion of delta vegetation in early successional stages creates mudflats or other sparsely vegetated areas that are important habitat for migratory waterfowl. Although less dramatic than the cases where flooding interrupts vegetational succession by washing away channel banks below mature forests, the periodic flooding of relatively flat delta areas is also an example of interrupted succession. Floodwaters will sometimes not only interrupt succession but also reverse it if flooding is of sufficient duration as, for example, where willows are drowned.

In the inner Mackenzie Delta, on upraised portions where flooding and sedimentation are minimal, peatlands are dominated by dwarf birch, Labrador tea and feather mosses. Such peaty areas are also associated with ice-wedge polygons (Reid and Calder 1977). Patterned ground features due to permafrost do not achieve a surface expression where rapid physical changes, such as deposition of sediment, occur regularly. Thus, the presence of polygons in peaty areas of the inner Mackenzie Delta indicates that disturbance by flooding and sedimentation has been minimal for hundreds of years.

After closure of the W.A.C. Bennett Dam in 1968, early successional changes from bare silt surfaces to willow shrubs occurred within a few years of continuous low water levels on the Peace-Athabasca Delta (Dirschl 1973). Three major conclusions were apparent: 1) successional events in the delta are mainly controlled by water regime; 2) vegetational succession with decreasing water levels proceeds rapidly in the initial stages, but more and more slowly through shrub and forest types; and 3) if there is a normally fluctuating hydrological cycle, sites directly influenced by fluctuating water levels tend to be held at early successional stages until ongoing deltaic processes, such as channel shifting or levee building, alter the local water regime (Dirschl et al. 1974).

Descriptions by early explorers and fur traders suggest that the overall appearance of the Peace-Athabasca Delta did not change in 300 years (Dirschl 1973). Changes in growth rates of trees indicate that over the 160 years previous to the Peace-Athabasca Delta study there have been times of drastic variation from average conditions. The maximum water level for mid-July has been about 1.6 m higher and the minimum 2.0 m lower than the long term average level (The Peace-Athabasca Delta Project Group 1972). With such fluctuations, periods of successional change from aquatic to woody vegetation and the reverse have both occurred in the past.

As a general rule in the Peace-Athabasca Delta, high water levels attained by past floods are sharply delineated by the lower limit of mature balsam poplar on the slopes of levees; below this level there are usually plant communities dominated by willow, alder, and sedge (Doherty and LaRoi 1973). Willow species are better adapted to partial and complete inundation by flood waters than are other woody species (Brink 1954). Among the non-woody species of the Peace-Athabasca Delta, marsh horsetail thrives where few other species could survive because of its high tolerance to prolonged flooding and to abrasive or erosive forces (Doherty and LaRoi 1973).

In general, the tolerance of willow to high water levels tends to preclude its elimination by flooding on many delta sites. Although there is little documentation of fire as a controlling factor in delta vegetational change, fire scars are common and widespread on willows and trees of the Peace-Athabasca Delta. It has been suggested that in the past fire was possibly a more effective control over willow vegetation types than was flooding (Cordes 1975).

In the case of sedge and reed grass vegetation types in the Peace-Athabasca Delta, changes are much more dramatic than they are with willow types after flooding. For example, the relatively high late summer water levels that were experienced in the delta in 1972, 1973, and 1974 indicated that there was little chance that either the sedge or reed grass meadows would be able to survive. Furthermore, it is unlikely that either sedge or reed grass could move to a higher position on the landscape by replacing other communities that presently occupy these sites. To do this, they would have to replace willow communities that are very tolerant to flooding. As of 1974, there was no indication that the older willow communities were being affected by the high water levels and no indication that sedge or reed grass were moving into the sites presently dominated by willow. If sedge and reed grass communities cannot survive in their present location and cannot move to a higher position on the landscape, there is only a very limited area in the delta where they can survive. Most of the area originally occupied by sedge and reed grass would be taken over by open water or emergent communities dominated by bulrush and whitetop in periods of continued high late summer water levels (Cordes 1975).

Successional sequences from aquatic vegetation to shrub or forest vegetation do not occur in all portions of the delta surfaces. For example, many lakes in the Mackenzie Delta have sufficient depth to prevent their freezing to the bottom in winter, and thermokarst activity occurs in the high ice-content silts and clays surrounding these lakes. Such activity widens the lake at the expense of the surrounding levees. Continual erosion and subsidence of the substrate makes establishment of aquatic plants impossible. As a result, there is no opportunity for succession from lake to aquatic vegetation and then to land vegetation (Gill 1973b).

On the Mackenzie Delta where normal outflow channels from delta lakes carry silt-laden flood waters into the lakes in spring, small reverse deltas form (Gill 1973b). The newest portions of those deltas, usually the points and edges, are vegetated with grasses, mainly **Arctophila fulva, Beckmannia syzigachne** and **Deschampsia**. As the small deltas are built up by additions of sediment and become better drained, the grasses are replaced by sedges and finally willows with a sedge understory (Gill 1973b, Reid and Calder 1977). The area of grasses may be a very narrow band on the edges of the small deltas. In small Saskatchewan wetlands, dominance by **Beckmannia syzigachne** tends to occur where there is an exposure of soil (Millar 1972). This grass is among a group of species that are reliable indicators of habitat instability. The continued presence of **Beckmannia syzigachne** is partly dependent upon the availability of new mineral soil, a condition provided in specialized habitats such as the reverse deltas.

B. Plant Succession on Non-deltaic Alluvial Sites

Changes to the land surface and drainage are relatively rapid in alluvial sites, in contrast to unflooded areas, with the result that it is difficult to think of alluvial plant communities except in terms of successional development (Raup 1946). The major factors that cause changes are physical damage by ice and the increasing elevation of surfaces over time due to the deposition of alluvium. Deposition has three important effects: internal drainage of soils increases with height above the river; the period of time that sites are under water during flooding is reduced with height above the river; and the yearly amount of sediments added to the surface decreases with height above the river (Annas 1977).

Non-deltaic sites described below include point bars, levees, floodplains, and several other alluvial landforms. Some of the habitats described here, such as point bars, are not exclusively limited to non-deltaic sites because they are associated with channel margins in both deltaic and non-deltaic portions of the basin. Some of the most detailed accounts of plant succession on point bars are from the work of Gill (1971) on the Mackenzie River Delta; portions of those accounts are summarized here because the processes involved also have general application to other alluvial sites along stream channels.

On deltaic sand-bed channels, the most common vegetation succession on point bars and levees begins with horsetail on the lowest and most frequently flooded surfaces near the river or channel. On successively higher surfaces, there is usually a sequence of willows, mixed alders and willows, balsam poplar, and finally white spruce. The summits of point bars and levees occupied by white spruce are the highest, best drained, and oldest habitats within the successional sequence (Figure 25). On gravelly channel margins, initial colonization by balsam poplar or willow is common, without a pioneer horsetail stage (Kellerhals and Gill 1973).

Sediment and vegetation appear to be strongly interrelated within the total floodplain system. Along the Beatton River in British Columbia, deposition of sediment averaged 6.1 cm/yr and totalled 2.5 m over a fifty year period in young balsam poplar stands. Underneath mature balsam poplar and young spruce, deposition averaged only 0.8 cm/yr. Mature spruce stands on alluvial sites are sometimes flooded but deposition of sediment tends to be negligible (Nanson and Beach 1977).

Sediment deposition is greater where the density of woody stems causes the rate of floodwater flow to decrease. In the Mackenzie Delta, willow stems increase the amount of sediment relative to that deposited in willow-free areas and in one flood 0.42 m of sediment was deposited in a dense stand of willows (Gill 1973a). Similar relationships were observed along the Beatton River where the highest rates of sedimentation occurred on the youngest surfaces, probably due to the combined effects of their proximity to the river

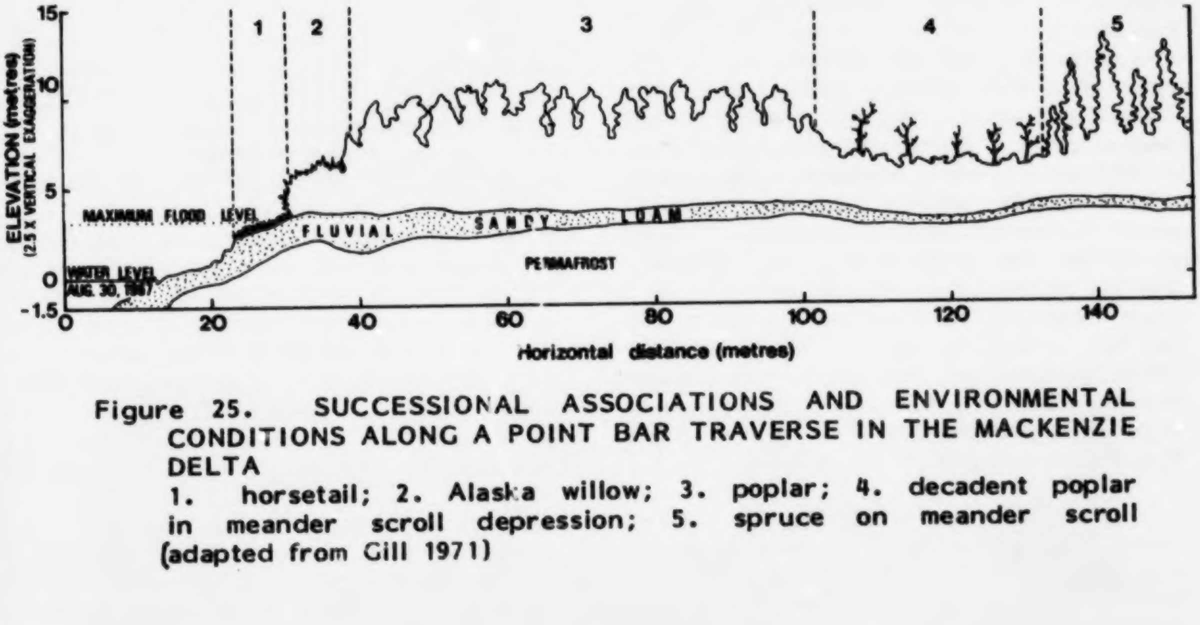
ELEVATION (metres)
(2.5 X VERTICAL EXAGGERATION)
15
10
5
0
-1.5
0
20
40
60
80
100
120
140
Horizontal distance (metres)
1
2
3
4
5
MAXIMUM FLOOD LEVEL
WATER LEVEL AUG. 30, 1967
FLUVIAL SANDY LOAM
PERMAFROST

Figure 25. SUCCESSIONAL ASSOCIATIONS AND ENVIRONMENTAL CONDITIONS ALONG A POINT BAR TRAVERSE IN THE MACKENZIE DELTA
1. horsetail; 2. Alaska willow; 3. poplar; 4. decadent poplar in meander scroll depression; 5. spruce on meander scroll (adapted from Gill 1971)

and the high densities of stems found there (Nanson and Beach 1977).

Few studies have attempted to establish the times required for different successional stages, but some figures are available from the Beatton River study area, where initial colonization of point bar surfaces is usually accomplished by balsam poplar. After the point bar surfaces are high enough to support tree species, young balsam poplar establish upon the surface until the oldest trees are approximately 40 years of age. Maximum density of balsam poplar stands occurs at 40 to 50 years after the point bar surface is first colonized, and then declines thereafter. When the surface has been raised above bankfull flood stage there is an abrupt decline in the rate of sedimentation, about 50 years after initiation of the successional sequence. White spruce seedlings establish in large numbers underneath balsam poplar stands approximately 60 years after sediment surfaces become available for occupancy by plants. Balsam poplar trees reach maturity and then begin to decline on surfaces 100 to 150 years in age. White spruce steadily replaces the declining balsam poplar, forming dense, usually pure stands approximately 200 years after the initial surface is established.

If undisturbed by fire, floods, or other events, mature white spruce forests may pass through several repetitive phases of overmature and decadent spruce being replaced by new spruce stands. To reach the point where a decadent white spruce stand is replaced by another white spruce stand may require up to 500 years, during which time the various successional phases are associated with distinctive differences in rate of sediment deposition, tree density, number of understory plant species, and development of a dense moss cover (Figure 26). In general, the rate of sediment deposition drops progressively over the first 50 years as succession advances from a horsetail plant community to balsam poplar with white spruce seedlings. Number of tree stems per unit area of land (tree density) is highest during the balsam poplar phase, from 50 to 200 years after succession is initiated. Numbers of understory species tend to be greatest around 100 years when the balsam poplar forest is well established with spruce seedlings present, and again around 400 years when decadent white spruce fall over to create openings in the forest canopy. It takes about 200 years for a dense moss cover to develop in the sequence of floodplain succession (Figure 26), as documented in the Beatton River study area (Nanson and Beach 1977).

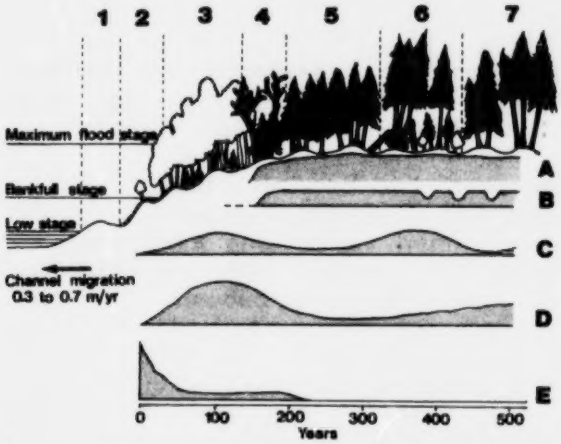

Figure 26. CHANGES IN SEDIMENTATION, FOREST COVER, UNDERSTORY SPECIES RICHNESS, TREE DENSITY, MOSS COVER, AND FROZEN GROUND IN RELATION TO CHANNEL MIGRATION ON THE BEATTON RIVER FLOODPLAIN IN NORTHEASTERN BRITISH COLUMBIA A. frozen ground; B. dense moss cover; C. number of understory species; D. tree density; E. rate of sediment deposition. 1. incipient ridge; 2. horsetail association; 3. balsam poplar with white spruce seedlings; 4. decadent poplar; 5. mature white spruce; 6. decadent white spruce with spruce seedlings; 7. mature white spruce (adapted from Nanson and Beach 1977)

The sequence of plant communities from channel margin to upper levee crest can vary according to the type of channel present, as documented by Gill (1971) for three types of channels in the Mackenzie Delta. The first type, actively shifting channels with abundant sediment deposition, have a common successional sequence of: horsetail; willow-horsetail; balsam poplar; and eventually white spruce (Figure 25). The second type, static channels, are not actively shifting and are flanked by levees in which plant associations exhibit only minor successional changes through time. The most common successional sequence is horsetail, willow-horsetail, and then willow. The willow stage is often not succeeded by any further stages. Sedimentation is not as rapid along this type of channel as it is along actively shifting channels; static channels occupy a greater area of the Mackenzie Delta than the active type. The third type of channel, referred to as stable channels, exhibits little sedimentation although it is subjected to flooding. The lowest zone is occupied by sedges, with willow-sedge the next plant community up from the channel edge. Further succession can result in balsam poplar and spruce vegetation types along stable channels, although such succession occurs at a very slow pace. Stable channels are the least common of the three types of channels in the Mackenzie Delta (Gill 1971).

The common successional progression of horsetail to willow is by-passed at the apexes of point bars in the Mackenzie Delta where initial colonization of sediment surfaces is by balsam poplar (Figure 27). These apexes receive the coarsest textured sediments and are believed to be too dry for horsetail and willow (Gill 1971). The same feature was recorded along the Beatton River in British Columbia where point bars were also initially colonized by balsam poplar (Nanson and Beach 1977).

In the successional sequences outlined above, if there are poor white spruce seed sources balsam poplar may be succeeded by only very sparse spruce. In such cases, the shrub understory will receive relatively more light and may be quite dense between the scattered individual spruce trees

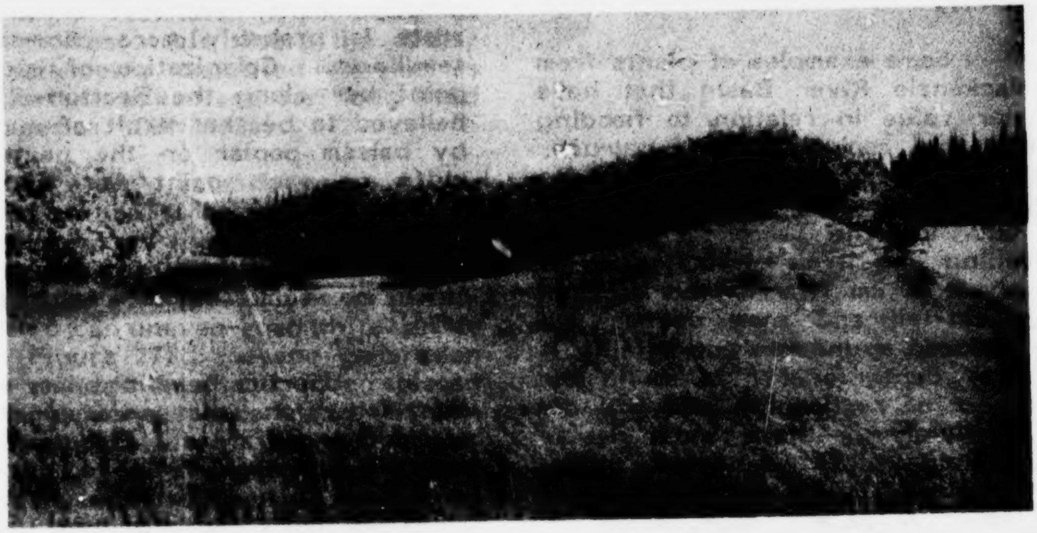

Figure 27. BALSAM POPLAR ON POINT BAR IN MACKENZIE DELTA (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

or spruce stands. Although the Liard River valley is known for its impressive white spruce stands, poorly stocked white spruce stands occur in some of the balsam poplar areas, especially where marsh horsetail is the dominant ground cover (Jeffrey 1964).

The ability of vegetation to establish on recently flooded areas or on newly deposited sediment is strongly influenced by the distinctive tolerances of individual species. For instance, water horsetail is able to successfully invade and dominate the newest portions of levees and point bars in the Mackenzie Delta. As well as being able to establish under conditions of extreme soil moisture, water horsetail is able to renew itself each year from rhizomes when above-ground plant parts are buried by alluvium. Soil profiles contain viable horsetail roots and rhizomes more than 30 cm below the surface. With the long and durable rhizomes that extend readily from buds of the previous year's growth, continued colonization of new alluvium by water horsetail is assured by rapid vegetative propagation (Gill 1971).

Some examples of plants from the Mackenzie River Basin that have indicator value in relation to flooding include the common great bulrush, cat-tail, some sedges, and some willows. The common great bulrush will die out in the second year of re-flooding and if the water depth is over about 40 cm (Harris and Marshall 1963); cat-tail and some sedges will show reduced abundance and vitality if the water depth is over 30 cm in the third year of re-flooding and will die out completely if these water levels are maintained into the fourth year. Well established willows are eliminated only after three or four years of continuous inundation of at least 60 cm depth (Doherty and LaRoi 1973).

In general, willow species are the woody plants most tolerant of flooding. On levees and point bars of Mackenzie Delta channels, Alaska willow quickly colonizes flood-prone levels which are also sites of rapid deposition (Gill 1973a). Alaska willow seeds are released shortly after receding floodwaters create a new seedbed; this species of willow is not tolerant of shade, and the open surfaces that it occupies are ideal habitat for maximum exposure to sunlight.

Alder is usually found above the level of most active flooding and sedimentation (Gill 1971, Annas 1977). In addition, the willow species found with alder may differ from the willow species that occupy the more commonly flooded zones (Gill 1971). Alder initially establishes by seed, but after it is established new stems readily regenerate from rootstocks after disturbance (Nanson and Beach 1977).

Balsam poplar may reproduce by seed, although vegetative propagation by means of suckers from roots is probably more common than seedlings. Colonization of each new point bar along the Beatton River is believed to be the result of suckering by balsam poplar on the next oldest ridge in each point bar succession (Nanson and Beach 1977). In contrast, Mackenzie Delta point bars appear to be colonized by seeds of balsam poplar since no suckering is evident (Gill 1971).

Spruce seedlings may become established on any successional stage of flood-prone areas. Floodwater does not immediately eliminate white spruce seedlings from lower, younger sites, since seedlings can withstand up to 14 days of inundation (Lees 1964). However, the sedimentation rate on lower sites is often too rapid for established spruce seedlings to survive (Gill 1971, Nanson and Beach 1977). Along the Beatton River, most white spruce establishment occurs over a 30 to 40 year period after there is a decline in sedimentation rates, although a 100 year spread in ages was found within the spruce stand studied (Nanson and Beach 1977). White spruce stands in the Mackenzie Delta are also of variable ages (Gill 1971).

The formation of adventitious roots on stems is a well documented response to flooding. Adventitious roots (Figure 12) are characteristic of woody species native to periodically flooded habitats and are usually regarded as an adaptation that confers tolerance to partial burial by sediment (Wagg 1964, Gill 1975). Willow, alder, balsam poplar, and white spruce are all able to produce adventitious roots which spread into newly deposited alluvium (Figure 18). Conditions are generally conducive to root growth in recent alluvium because it is better aerated than older and lower sediments (North 1976). In areas of permafrost, where older rooting zones become increasingly restricted from below as the permafrost table rises, the ability to exploit newly deposited alluvium is an important advantage for long-lived plant species (Gill 1973a).

After establishment of a forest dominated by white spruce, further successional changes are possible. Along the Beatton River, the initial white spruce stand is gradually replaced by an uneven-aged white spruce stand (Figure 27). Second generation spruce stands may, in turn, be replaced by a third white spruce stand (Nanson and Beach 1977). In the Athabasca-Great Slave Lake area, Raup (1946) observed that spruce forests on alluvial sites appeared to perpetuate themselves if not disturbed. However, along the Mackenzie River valley, Reid and Janz (1974) found little regeneration of white spruce under existing white spruce stands and stated that existing spruce regeneration was insufficient to restock the stands.

In the absence of disturbances, such as fire or interrupted succession as a result of erosion, floodplain white spruce stands can evolve to a black spruce-moss type (Annas 1977). On older terraces along the Mackenzie River, a black spruce-feathermoss type occurs (Reid and Janz 1974). Similarly, along the Chena River in Alaska, there is a forest succession and soil development sequence from alluvial vegetation to a black spruce forest; the latter is underlain by permafrost similar to that on adjacent non-fluvial uplands (Figure 28). As balsam poplar is replaced by white spruce, a continuous and thick moss layer develops. The layer of moss and accumulated organic material acts as a more efficient insulator during summer than it does in winter, with the result that soil temperatures are relatively cool

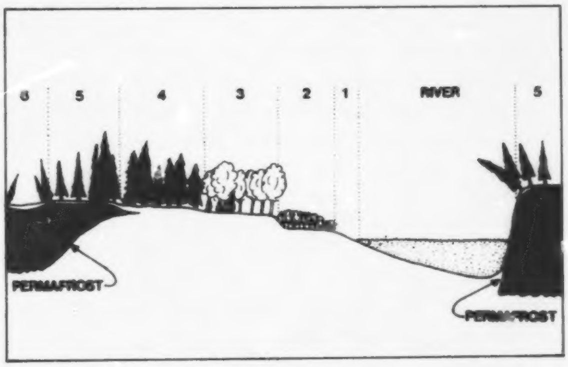

Figure 28. TYPICAL VEGETATION ZONES AND PERMAFROST DISTRIBUTION ACROSS A MEANDER ON THE CHENA RIVER, ALASKA
1. bare silt; 2. willow; 3. balsam poplar; 4. white spruce; 5. black spruce; 6. bog (adapted from Viereck 1970)

beneath the moss in summer. Eventually a permafrost zone develops and it interferes with drainage to create wetter soil conditions. With cooler and wetter soil conditions, a restricted rooting zone, and resulting decrease in available nutrients, conditions are more favourable for black spruce, ericaceous shrubs and **Sphagnum** mosses than they are for white spruce (Viereck 1970). Along the Beatton River floodplain in northeastern British Columbia, frozen ground is present only under mature white spruce stands. One of the suggested reasons is that as spruce trees become more dominant and less sunlight reaches the ground surface, frozen ground is able to establish itself (Nanson and Beach 1977).

In point bars of the Mackenzie Delta, ground ice may be present beneath all vegetation types. However, due to the coarse nature of point bar sediments and the heat energy received through the deciduous canopy, areas underneath poplar stands have a warmer and deeper active layer than most other sites in the delta. Soil warming occurs earlier in the spring underneath poplar stands than it does under other vegetation types and allows poplar to break winter dormancy earlier than other plant species (Gill 1972c). There is widespread occurrence of ground ice on point bars along shifting channels in the Mackenzie Delta, but some areas of permafrost-free soil occur (Gill 1973a). Soils without permafrost are usually below a willow-horsetail vegetation type, which is found over a significant portion (8%) of the delta. Several factors may contribute to the presence of such unfrozen ground, including the influence of adjacent channels in which average annual temperature is above freezing and the insulation provided by snow drifts within and on the edges of willow stands.

Successional changes such as those outlined in the examples above require the absence of an intervening disturbance. Continual replacement of mature point bars and levees normally does not allow enough time for successional changes beyond mature white spruce in the Mackenzie Delta (Gill 1973). In contrast, some alluvial sites along the Beatton River in northern British Columbia have not been disturbed by channel migration for 700 years (Nanson and Beach 1977), but along the nearby Muskwa River, it was estimated that floodplain surfaces were generally eroded by channel migration before they reached 400 years of age (Annas 1977). In ecological terms, the interruption of a successional sequence by channel erosion (Figure 29) is a catastrophic event. However, it has been suggested that continual disturbances such as floods that expose mineral soil are required for establishment of alluvial white spruce stands (Reid and Janz 1974).

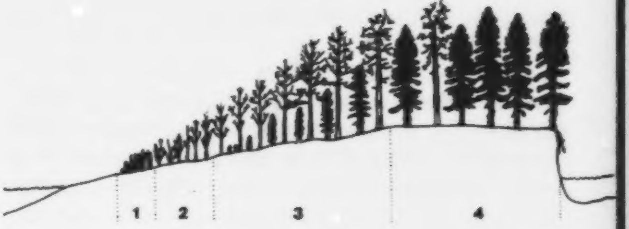

Figure 29. VEGETATION ZONES AND INTERRUPTED FOREST SUCCESSION ON A FLOODPLAIN IN NORTHEASTERN BRITISH COLUMBIA
1. willow; 2. alder; 3. balsam poplar; 4. white spruce on young terrace (adapted from Annas 1977)

On the west side of the Mackenzie River, catastrophic floods occurred along the Hume River during the summers of 1970 and 1971. Both floods were believed to have a return frequency of 150 years. Mature trees in both balsam poplar and white spruce stands were toppled but not carried away. The humus layer underneath white spruce stands was badly disturbed. In balsam poplar stands, alder, willow, and balsam poplar suckers were present in great abundance during vegetation studies in the Hume River valley in 1972 and 1973; in white spruce stands, white spruce seedlings and alder shoots as well as a few scattered herbs were regenerating (Reid 1974).

The relative absence of fire as a disturbance on alluvial sites compared to other sites on uplands is believed to be responsible for the great ages of white spruce trees found on alluvial sites (Kerfoot 1975, Annas 1977). Reasons for the observed lack of fires include: floodplains, river meanders, and oxbow lakes that act as barriers to the spread of fires; the frequent presence of seepage sites at the base of steep slopes adjacent to alluvial sites; a large amount of exposed mineral soil after flooding; and a relative lack of fuel on the floodplain forest floor (Annas 1977, Nanson and Beach 1977).

Independently of the overstory species that dominate the distinctive bands of vegetation along channels and other flood-prone areas, there are often distinct differences in understory species that indicate differences in flood frequency or sedimentation rate. Willow, mixed alder and willow, and balsam poplar stands that are frequently flooded usually have an understory dominated by horsetail (Jeffrey 1964, Forest Management Institute 1974, Reid and Janz 1974). Less frequently flooded balsam poplar stands often have a dense shrub understory of several species of willow, alder, red-osier dogwood, rose, and white spruce seedlings (Raup 1946, Gill 1972c). Vascular plants generally do not form a lush and varied herb layer until sedimentation rates are low and a balsam poplar stand is well established (Gill 1972c, Nanson and Beach 1977). Several species of mosses may be present on fallen logs and around the bases of tree trunks in the balsam poplar phase of a succession sequence, although little if any moss cover is present on the ground until sedimentation is negligible and the spruce phase is reached (Gill 1972c, Annas 1977).

There tends to be a decline in number of understory species as white spruce becomes dominant (Figure 26). If the stand of spruce is dense and allows very little sunlight to reach lower levels, the shrub layer may be sparse or non-existent (Raup 1946, Nanson and Beach 1977), yet other descriptions of white spruce stands refer to a dense shrub layer (Gill 1971, Annas 1977). The herb layer may also become relatively sparse in spruce stands (Nanson and Beach 1977), although the numbers of species may be greater in white spruce stands than in adjacent balsam poplar stands (Annas 1977). A complete and often luxuriant ground cover of mosses, particularly feather mosses, is usually present underneath spruce stands (Reid and Janz 1974, Annas 1977).

An analysis of understory species in the different successional stages along the Beatton River resulted in identification of three species groups (Nanson and Beach 1977). The initial group represented early colonizing species on exposed floodplain surfaces adjacent to the river channel, involving surfaces as great as 130 years of age; the second group represented those species that occur primarily under the spruce canopy, and also species common to both spruce and poplar zones; the third group was only present under stands of over-mature and second generation spruce. In general, white spruce on alluvial sites (Figure 24) can usually be taken as a boundary marker above which sedimentation is greatly reduced; although flooding may occur on zones dominated by white spruce, sedimentation is negligible. Species groupings such as those outlined above can be used as indicators of not only successional phases but also certain hydrological features such as sedimentation rate or time since the last flood.

In the study area described by Nanson and Beach (1977), white spruce and balsam poplar occur on both the ridges and swales of point bars. Growth of white spruce is better on ridge tops, due to improved drainage of these sites (Nanson and Beach 1977). Swales are present behind nearly all point bars and adjacent down-channel slip-off slopes examined in the Mackenzie Delta (Gill 1972c). Ponding occurs in these swales and they remain flooded for much of the summer. Most of the water in these ponds is from snowmelt runoff or spring rains, and only occasionally from inundation by spring floods. The bottoms of swales are sealed by both permafrost and layers of fine sediment. Vegetation in these depressions consists of variable stands of moisture-tolerant willow and alder. Dead balsam poplar in swales are believed to be the result of rising water tables which occur after such depressions are cut off from the main channel (Gill 1972c).

Although many low areas behind levees are flooded by waters of average spring level, areas subjected to only rare flooding eventually develop to an open black spruce-Labrador tea-bearbearry type (Reid and Janz 1974). This type is similar to the typical subarctic forests of black spruce-lichen that occur on upland sites within the northern Mackenzie River Basin (Zoltai and Pettapiece 1973). The black spruce-Labrador tea-bearberry vegetation types behind levees are rarely reached by annual floods and, if flooded, do not receive a great deal of sediment. The microtopography of these sites is often characterized by mineral soil hummocks with organic layers 20 to 30 cm thick between the hummocks, a condition that is typical for all imperfectly drained sites in the northern Mackenzie Basin (S.C. Zoltai, pers. comm. 1981). Similar muskeg vegetation has been described along the Athabasca River in Alberta around oxbow lakes or in other areas where drainage is cut off from nearby river channels (Raup 1946).

The examples summarized above indicate that there are considerable variations in successional trends on alluvial sites within the Mackenzie River Basin in response to a variety of factors, including regional climate, disturbances such as channel migration or catastrophic floods, and variability in types of alluvial landforms. One other important variable that is not emphasized in the physical factors listed above is the influence of species distribution upon successional sequences. An example of the latter is provided by sandbar willow which is usually the first woody species to establish on sandbars and newly exposed alluvial surfaces south of the Mackenzie Delta (Porsild and Cody 1980). In contrast, within the Mackenzie Delta, Alaska willow is the dominant woody species on almost all new surfaces subject to rapid sedimentation (Gill 1972c).

The general trends common to vegetational succession on most alluvial sites can be summarized as follows. If a surface is sand rather than gravel as soon as the surface is exposed above average summer water levels, colonization by plants, usually horsetail, occurs. When further deposits of sediment raise the surface sufficiently, willow becomes established. The horsetail and willow zones are subject to the heaviest flooding and sediment deposition. When the surface is raised above the bankfull flood stage, alder, balsam poplar, and white spruce become established. As the balsam poplar mature and die they are replaced by white spruce. Willow and alder may remain as understory shrubs through subsequent stages. However, once the site is beyond the reach of even the highest flood levels, an open black spruce-lichen-Labrador tea forest will develop.

C. Productivity of Vegetation on Alluvial Sites

There is a considerable amount of background information available on primary productivity rates but little of it provides direct comparisons between alluvial sites and adjacent non-alluvial sites. Little of the available information is derived from study sites within the Mackenzie River Basin. Consequently, the review below draws upon principles of production ecology that are applicable, in theory, to a wide range of ecosystems. The emphasis is upon information from alluvial sites wherever possible, even though many of the data are from areas outside the Mackenzie River Basin.

Primary productivity refers to the rate at which radiant energy from sunshine is stored by the photosynthetic activities of green plants in the form of organic substances (Odum 1971). For terrestrial ecosystems, primary productivity measurements are commonly expressed as mass of organic matter fixed per unit area of land per year, for example metric tons per hectare per year (t/ha/yr). In the case of trees, productivity can be approximated on a volume basis such as cubic meters of wood per hectare per year (m^3/ha/yr). Productivity refers to the rate at which organic matter accumulates, and should not be confused with standing crop, which is the amount of organic matter present at a given time (Whittaker 1970). Standing crop, which is also referred to as biomass, is normally expressed as the mass of organic matter present on a unit area of land.

The distinction between productivity and standing crop is of particular significance in those alluvial sites that are subject to interrupted succession during periodic destruction by flood-induced erosion. A high productivity, with rapid growth rates and rapid accumulation of organic matter, may never be expressed as a high standing crop if the ecosystem is physically destroyed by a flood before a high standing crop can accumulate. For example, storm floods in rivers that drain the Mackenzie Mountains have been known to flatten and uproot large spruce trees on islands (MacKay et al. 1973). In ordinary circumstances, the presence of a high standing crop, for example a large timber volume per unit area of land, is an indication of high productivity; after passage of a destructive flood, however, the standing crop of live trees may be virtually zero but primary productivity (the rate at which organic matter accumulates on the site) could be undiminished, or perhaps even increased. The same principle would also apply in certain sites without the intervention of an extreme flood. For example, point bars are regularly maintained at early successional stages, by annual flooding and sedimentation, with no chance for a large standing crop to accumulate.

In a world-wide comparison, Whittaker (1970) found that some of the plant communities with the highest productivity included early successional communities. If the rate at which organic matter is produced exceeds the rate at which it is decomposed, biomass of the community increases, as in successional stages of vegetational development. If the rates of production and decomposition are in balance, the community is in a steady state, as is the case for climax plant communities. In many forest ecosystems, maximum productivity occurs during one of the stages prior to climax (Whittaker 1970). Ovington (1962) described a relatively rapid increase in productivity for a Scotch pine plantation until maximum productivity was reached at about 20 years of age. The high level of productivity was maintained until the trees were about 35 years old, after which productivity declined rapidly. High productivity may occur when physical factors are favourable and especially when there are energy subsidies from outside the system (Odum 1971). These subsidies generally involve combinations of high moisture availability, relatively warm temperature, and continuing nutrient replenishment (Whittaker 1970).

Outside of the Mackenzie River Basin, one of the most specific sources of comparative productivity data for alluvial and adjacent non-alluvial sites is from a study in Illinois where primary productivity of three vegetation zones was related to varying degrees of flooding along a river floodplain (Johnson and Bell 1976). Only the lower edge of the upland zone in the Illinois study area was subject to flooding, and the portion that was flooded was under water less than 0.5% of the time during the growing season; a transition zone was flooded 0.5% to 3.0% of the time; and the floodplain zone was flooded 3% to 25% of the time. Above-ground production estimates for the three zones were: floodplain 12.5 t/ha/yr; transition zone 8.0 t/ha/yr; and upland zone 10.9 t/ha/yr. The most rapid growth rate of any of the tree species in the study area was recorded for the dominant tree in the most frequently flooded zone. The reasons for higher productivity in this zone were believed to be fertile soils and abundant soil moisture. Reasons for the relatively high productivity of the upland zone were not specified (Johnson and Bell 1976).

On the Missouri River floodplain in North Dakota, Johnson et al. (1976) found that soils of the youngest portions of the floodplain were generally sandy and low in organic matter. Soil nutrient content and available water capacity in the older portions of the floodplain were higher than on the younger parts of the floodplain because of higher organic matter content and repeated inputs of nutrients from silt during past floods. In addition to the inputs of silt, there was a high frequency of nitrogen-fixing herbs in young stands which contributed to the observed build-up of soil nitrogen (Johnson et al. 1976). Similar observations were made in the Mackenzie Delta where there is a high proportion of the legume, sweet vetch, in balsam poplar stands (Gill 1971). Sweet vetch contributes to an increased soil nitrogen level which is reflected in the plant species diversity on such sites (Gill 1971).

In three alluvial meadow plant communities that formed part of a flooded meadow complex adjacent to two rivers in Czechoslovakia, a community dominated by fescue was found on local elevations and was rarely flooded; a foxtail community was flooded regularly; a manna-grass community was situated at the base of a depression and was flooded for a relatively long period. The fescue and foxtail communities were mowed for hay once or twice a year, while the manna-grass community was not mowed. In the year in which measurements were made, the foxtail and manna-grass communities were flooded for three separate periods for at least a week in duration at the end of April, May and August. Above ground productivity in the fescue community was 7.5 t/ha/yr, in the foxtail community 8.5 t/ha/yr, and in the manna-grass community 14.6 t/ha/yr. Litter carried by the floods was deposited in the two flood-prone communities; the manna-grass community received the greatest amount of litter. The amount of litter deposited after a flood could surpass the amount of plant matter which a given plant community was able to produce in a corresponding period of time. In general, increased primary productivity was associated with increased flooding; with increased productivity there tends to be more litter accumulation, higher soil organic matter content, and higher soil nitrogen content (Tesarova 1976).

The main factors thought to influence productive capacity of forest land in the Mackenzie River valley are texture, mineralogical composition, depth to underlying bedrock, local topography, drainage conditions of soil, and regional climate (Reid and Janz 1974). Comparisons of forests in Manitoba, Saskatchewan, Alberta, and in the southern and central portions of the Mackenzie River valley show a drop in productivity in all terrain types as one progresses from south to north. In southern portions of the Mackenzie River valley, white spruce may reach heights of 37 m, while in the northern portions of the valley, growth is slower and maximum heights seldom exceed 21 m.

Terrain types that do not become water-logged are generally more productive than poorly drained terrain types. The major differences in productivity between the middle and southern portions of the Mackenzie River valley appear to be related to distribution of permafrost. Thus, productivity is higher in the southern part of the valley where active layers are thicker and the soils generally warmer. In general, higher forest productivity occurs on levees and terraces of alluvial meander plains of the major rivers. Depressional areas with saturated soils and thin active layers have very low forest productivities.

Within the Mackenzie River Basin, some alluvial sites are known to have a relatively high forest and agricultural productivity but they make up a small percentage of the total area (Reid and Janz 1974). Along the Liard and South Nahanni rivers, merchantable timber usually occurs within a few kilometers of the river and on some tributaries is restricted to alluvial flats immediately adjacent to the river (Hirvonen 1968). White spruce, which is the most desirable timber species, achieves the best growth on alluvial soils of floodplains where it grows in pure stands or mixed with balsam poplar (Jeffrey 1964). Along the Liard River in the Yukon, the most productive forest site type occurs on recent alluvium or along drainage channels on till slopes that are imperfectly to well drained. The second most productive site type occurs on river terraces or moderate till slopes that are well drained (Peaker 1968). In the Yukon and Northwest Territories, these relatively productive non-alluvial sites occupy a much smaller percentage of the total area than alluvial sites of comparable productivity.

In the Sans Sault-Norman Wells area, the highest forest productivity is found on levees of alluvial floodplains of the major rivers. Some alluvial sites have low productivity due to poor drainage and a shallow active layer. Trees on non-alluvial sites with good soil drainage and a deeper active layer may achieve productivity comparable to that on alluvial sites (Table 1). The growth of commercial forests in the Sans Sault-Norman Wells area is

TABLE 1. FOREST PRODUCTIVITY, IN TERMS OF AVERAGE MEAN ANNUAL INCREMENTS (m^3/ha/yr), FOR BALSAM POPLAR, WHITE SPRUCE, BLACK SPRUCE AND WHITE BIRCH IN VEGETATION UNITS OF THE MACKENZIE RIVER VALLEY (adapted from Reid 1974).

Terrain types	Vegetation units	Average mean annual increment (m^3/ha/yr)
A. **Alluvial**		
Low terrace	balsam poplar-grey alder-horsetail	2.53
Low terrace	white spruce-feather moss	1.72
Backswamp	black spruce-feather moss	0.32
Old terrace	open black spruce-Labrador tea-reindeer lichen	0.18
B. **Non-alluvial**		
Drumlin	black spruce-white birch-mountain cranberry	0.54
Thin drift over bedrock	white spruce-white birch-green alder	2.11

restricted to small portions of better drained alluvial levees, till and lacustrine deposits (Reid 1974).

A soil survey of the Liard River valley and part of the Mackenzie River valley described the soils of the most recent floodplain as the most productive forest land (Rostad et al. 1976). The soils were fertile because of a buried organic matter, neutral to mildly alkaline pH, and favourable moisture status. Although the soils of recent floodplains tend to be coarse textured, a reliable moisture supply is assured because of their proximity to river water levels.

Alluvial soils of the Peace and Liard river valleys in British Columbia are considered to be very productive (Young and Alley 1978, Canadian Bio Resources Consultants Ltd. 1979); alluvial soils on terraces of the Peace River valley have favourable nutrient contents and water-holding capabilities, and loamy sand or sandy loam textures that make them highly suited to intensive cultivation (Canadian Bio Resources Consultants Ltd. 1979). In contrast, gravel bars, beaches, and major river scars have little or no topsoil, are excessively stony, and have no agricultural capability.

In the Slave River lowland, two basic types of meadows, wet and dry, are used by bison. These two types are not exclusive to the most recent floodplain of the Slave River and commonly occur in areas that are physically and hydrologically removed from the modern Slave River. Most of the wet meadow plant cover is provided by sedges and grasses. The dominant sedges are **Carex atherodes**, **C. rostrata**, and **C. aquatilit**. The most common grasses in wet meadows are reed bentgrass, whitetop, and manna-grass. In dry meadows, most of the cover is provided by grasses and forbs, with northern reed grass being the most common species and wire rush the second most common. The figures below summarize productivity estimates for such meadows (Reynolds et al. 1978).

Annual production estimates

Wet meadow	1974	4.5 t/ha/yr
	1975	4.3 t/ha/yr
Dry meadow	1974	2.7 t/ha/yr
	1975	1.9 t/ha/yr

Within the Peace-Athabasca Delta, Cordes (1975) stressed that sedge and reed bentgrass meadows were largely responsible for the apparent high primary productivity of that delta. Such areas of high productivity, if they have not succeeded to willows, are particularly important when they occur close to sites that offer other attractions to wildlife species. In the case of the Peace-Athabasca Delta, the periodic flooding and drowning of plant communities of early successional stages is an important factor in maintenance of mudflats and open areas that attract staging waterfowl; the mix of such specialized habitats and nearby areas of high primary productivity is a contributing factor to the biological importance of northern deltas.

CHAPTER VI

WILDLIFE AND WILDLIFE HABITAT IN ALLUVIAL AREAS

The discussion of wildlife in alluvial areas is divided into two major subdivisions - one dealing with major deltas within the Mackenzie River Basin and the other with non-deltaic alluvial sites within the basin - in recognition of the distinctive wildlife and habitat conditions that exist in those two classes of flood-prone landscapes. The focus is on birds, aquatic furbearers, terrestrial furbearers, and ungulates for all areas considered, with a separate discussion of marine mammals in relation to the Mackenzie Delta.

Later sections of the chapter deal with comparisons of wildlife and habitat features in alluvial and non-alluvial areas, and nutrient value of vegetation used by wildlife. Literature reviewed as background material for this chapter included reports of consultants and government scientists who had investigated the effects of a Mackenzie Valley pipeline, of the Athabasca Oil Sands Environmental Research Program, the Peace-Athabasca Delta Project, the work of Dr. Don Gill, and various reports of consultants relating to the effects of hydroelectric projects within the basin.

A. Wildlife and Wildlife Habitat of Major Delta Areas

The deltas of the Peace-Athabasca, Slave, and Mackenzie rivers are the three largest alluvial areas in the Mackenzie River Basin. Their importance to wildlife is underscored by the fact that few other concentrations of wetlands occur in the basin. The variety of habitats produced by hydrologic and physical processes particular to deltas also contribute to their attractiveness for wildlife.

In the subsections below, wildlife species groups are discussed individually and the importance of each delta to the group is considered.

1. Birds: Because of their economic importance and the continental nature of many populations, waterfowl have been the focus of much northern research. However, in assessing the value of northern deltas to populations of waterfowl, extrinsic factors which influence use must be considered. Numbers of birds using an area in any year may be partly a reflection of conditions far to the north or south. Northern deltas become particularly important during years of drought on the prairies, when non-nesting birds that were destined for the prairie potholes fly over the inhospitable drylands and spend the summer on more permanent northern wetlands (Hennan 1973). In years of early snowfall and freezeup in the north, birds of the Arctic must stop more frequently on their way south than they do in late autumns of good weather (Patterson 1974). Numbers of birds observed at intermediate staging sites may be high in years of poor autumn weather on the arctic coast.

Different physical processes produce the habitats favoured by birds during migrating and nesting periods. Therefore, migration and production are discussed separately.

a. Peace-Athabasca Delta: Of the three deltas, the Peace-Athabasca supports the waterfowl populations which have been surveyed most intensively and over the longest continuous period. Many of the general comments below probably apply to all three deltas.

Migrating waterfowl begin to stage on the Peace-Athabasca Delta as soon as ice starts to break up in spring. Staging may begin as early as late April and last until late May. Large numbers of ducks, geese and swans stop on the delta each spring (Figure 30). Estimates of the numbers of birds using the delta in spring of some years have been as high as 432 500 ducks, and 145 000 geese and swans (Hennan 1973, Hennan and Ambrock 1977).

More than half of the geese present on the delta in spring can be expected to be lesser snow geese and about one quarter Canada geese. Geese and swans are found on and adjacent to mudflats and immature meadow edges. Dabbling ducks are seen most often along habitat edges classified as mudflat, meadow, immature meadow, and emergent. Diving ducks are associated with habitat edges of emergents, tall shrubs, meadows, and low shrubs (Hennan 1973). Spring staging on the delta occurs while water levels are at seasonally high levels caused by local runoff or ice dams.

Fall staging waterfowl begin to arrive on the Peace-Athabasca Delta in mid-August and staging continues until mid-October. The fall population includes the annual production and may reach 1 000 000 to 1 500 000 waterfowl, including 110 000 to 165 000 geese in some years. Numbers of birds per shoreline kilometer were as high as 3 050 dabblers 435 geese, and 50 swans in an exceptional year (Hennan 1973).

Numbers of staging waterfowl on the delta in spring and fall are high or moderately high under all but extreme flood conditions. Highest numbers were recorded (in 1971) after three years without flooding. However, in years when high water extends beyond normal shorelines into willow or forested habitats, numbers of staging birds are low (Hennan and Ambrock 1977). The important factor seems to be availability of open dryland edges, particularly mudflats or immature meadows (Hennan 1973). Although it appears from the above discussion that

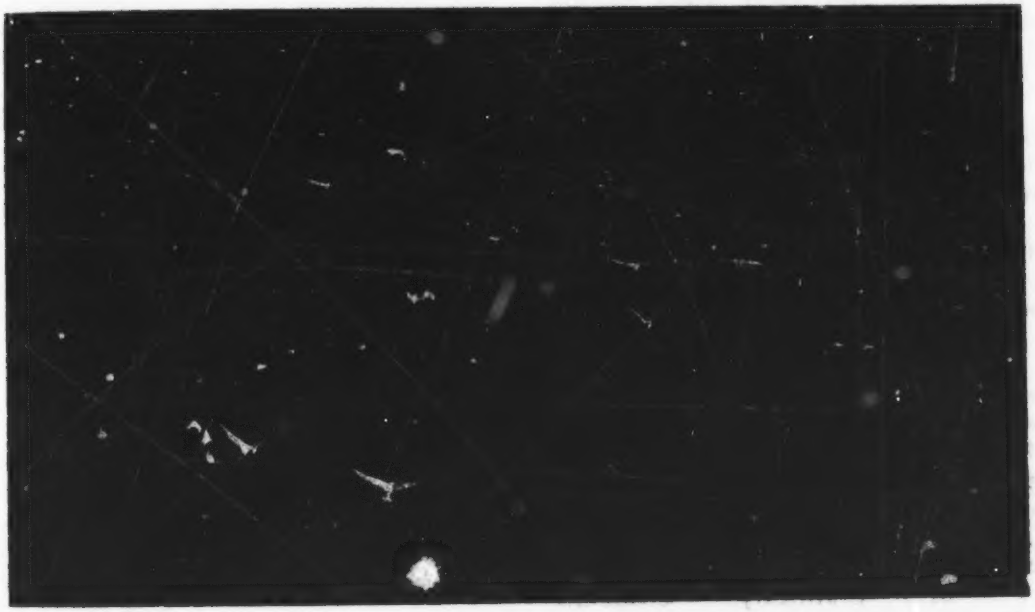

Figure 30. CONCENTRATIONS OF WHISTLING SWANS STAGING ON THE PEACE-ATHABASCA DELTA (Courtesy of L.M. Allison, Salix Enterprises Ltd., Cowley, Alberta)

stable low water levels would favour use of the delta by large numbers of staging birds, it must be remembered that periodic flooding and drowning of early succession plant communities, as described in Chapter V, is required to maintain the mudflats and meadows that attract staging waterfowl.

In years when water levels are low on the delta, staging birds are observed in mudflat and immature meadow sites. When water levels are higher, birds are more commonly observed on the margins of meadow and low shrub communities. From that, it might be thought that birds are distributed differently over the delta from year to year. However, on the Peace-Athabasca Delta, certain geographic areas seem to be more important than other areas to staging waterfowl (Soper 1933, Hennan 1973). Habitat choice seems to be largely a function of water level at important resting sites. Whether use of specific areas is "traditional" or whether some particular feature is being selected is not known. Heavily used areas may simply be those having the most extensive exposed mudflats when water levels are low.

The Peace-Athabasca Delta supports 14 species of nesting and moulting ducks and a few Canada geese (Hennan 1973). Because each species has slightly different habitat requirements, only generalizations about waterfowl production on the delta can be made.

Nesting pairs of dabbling ducks were most commonly seen along meadow, emergent, and tall-shrub shoreline habitats, while diving species were found adjacent to tall shrub, emergent, and low shrub habitat types, most commonly in restricted drainage areas (Hennan 1973). The variety of distinctly different vegetation types within small areas of the delta makes it difficult to ascribe habitat preferences from data, like those above, collected during aerial surveys. Dabbling ducks in particular may nest a long way from the water. Some of those observed near tall shrub shorelines may actually nest on sedge or grass meadows behind a levee.

In 1971, an estimated total of 162 700 breeding pairs of ducks occupied 5 180 km^2, a density of 31 pairs per km^2 (Hennan 1973). Restricted drainage areas supported the largest densities of breeding pairs, and by inference, the greatest proportion of annual duck production on the delta. Restricted drainages are those areas which do not have an open connection with the major lakes or channels of the delta. Such areas are not subject to water level fluctuations as extreme as open systems. For optimum waterfowl production, nesting habitat must be maintained through the period from late April to 31 July. A moderate recession in water levels would not significantly reduce nesting success. However, rises in water level during nesting can cause serious losses by drowning nests, particularly those of divers which normally nest closer to the water edge than dabblers (Hennan 1973). There were two periods of possible flooding that could interfere with nesting waterfowl on the Peace-Athabasca Delta under the natural hydrologic regime before construction of the W.A.C. Bennett Dam. The first occurred from local runoff and ice jams during breakup. The second occurred when mountain snowmelt reached the delta in late June or early July.

Moulting populations of waterfowl include post-breeding and non-breeding delta residents as well as sub-adult, non-breeding, post-breeding, and unsuccessful immigrants from other areas. The numbers of moulters may approach 500 000 ducks (Hennan 1973).

Under a natural water regime, waterfowl production on the Peace-Athabasca Delta was far below its potential because of flooding in spring (Hennan 1973). However, it would not be possible to imagine a realistic delta flow regime which met all the requirements of both nesting and staging birds. In years of very low water levels, numbers of migrants and production both seem to be high. However, periodic flooding is also necessary to maintain the variety of habitats attractive to nesting birds, although optimum production habitat results after several years of low water levels (Hennan 1973).

Remedial measures undertaken to offset the effects of the W.A.C. Bennett Dam on wildlife and wildlife habitats of the Peace-Athabasca Delta have not been successful (Hennan and Ambrock 1977, Cordes 1975, Poll and Stelfox 1978a, 1978b). Both staging and nesting waterfowl suffer when floodwaters reaching the delta are not allowed to recede quickly. Since 1971, an exceptionally dry year, populations of birds using the delta have remained relatively low.

Hennan and Ambrock (1977) predicted a relationship between water regime on the delta in any given year and relative use by waterfowl (Table 2).

In summary, the Peace-Athabasca Delta has national and international significance for waterfowl. Most of the birds using the delta are from the Central and Mississippi Flyways although all four flyways are represented (Figure 31).

Table 2. An estimation of the relationship of waterfowl densities and numbers to various water-level regimes in the Peace-Athabasca Delta, 1971-76 (based on census results).*

	Densities per shoreline mile			Numbers
Water Regime and Habitat	No. of Spring Staging Birds	No. of Breeding Pairs	No. of Broods	Fall-staging (thousands)
1. GENERALLY LOW (ca 683 ft [204.9 m] a.s.l.): Lake Athabasca at Ft. Chipewyan				
(a) No extremely early summer water level rise (following 2 or more years of low to moderate levels)	20	6+	3-4	1,000+
(b) Substantial early summer floods	20	6+	1-2	
(i) with fall recession				800
(ii) without fall recession				700
2. GENERALLY MODERATE (ca 685-687 ft [205.5-206.1 m])				
(a) No extremely early summer water level rise	12-13	3-5	2-3	
(i) with fall recession				700
(ii) without fall recession				500
(b) Substantial early summer floods	12-13	3-5	1	
(i) with fall recession				500
(ii) without fall recession				300
3. GENERALLY HIGH (ca 687-689 ft [206.1-206.7 m])				
(a) No extremely early summer water level rise	3-6	2-3	1	
(i) with fall recession				300
(ii) without fall recession				200
(b) Substantial early-summer floods	3-6	203	>0.5	
(i) with fall recession				200
(ii) without fall recession				100

* Hennan, E.G. and K.R. Ambrock (1977).

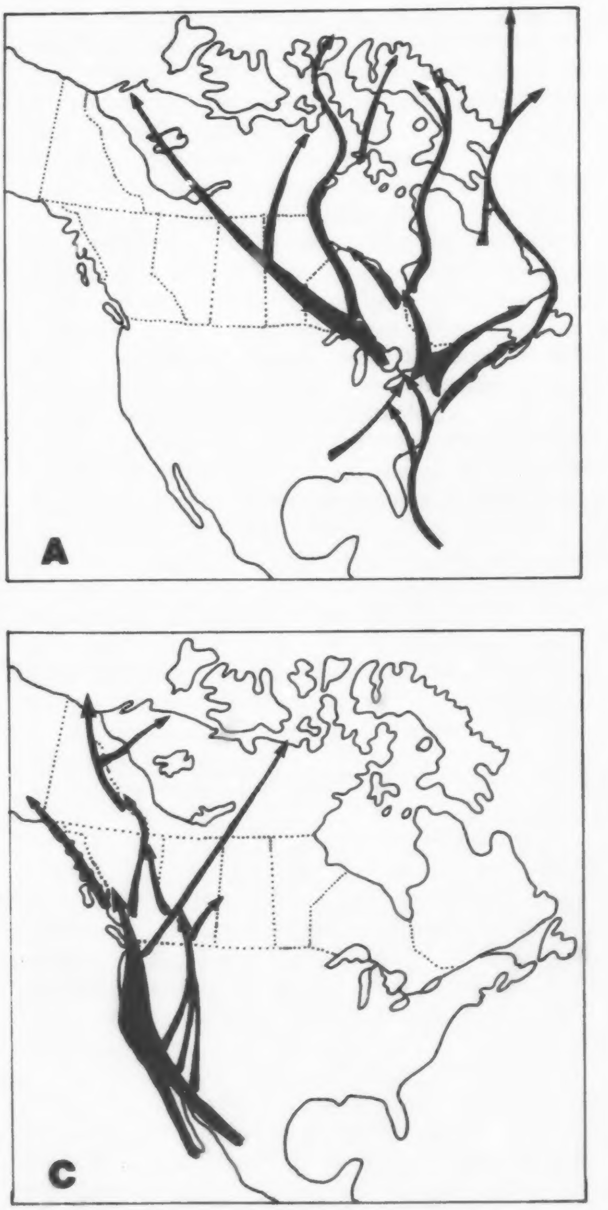

Figure 31. MAJOR NORTH AMERICAN FLYWAYS OF MIGRATORY WATERFOWL
A. Atlantic flyway; B. Central flyway; C. Pacific flyway; D. Mississippi flyway (adapted from The Peace Athabasca Delta Project Group 1972)

Migrant birds continue north from the delta through the basin (Figure 32). The Peace-Athabasca is the most important northern delta for waterfowl production because of its variety of habitat types and its frost-free season which is long enough for re-nesting if neccesary (Soper 1951, Hennan 1973). This delta is known to be a retreat for prairie birds in years of drought. Hennan (1973) speculated that as wetland conditions in the prairies have deteriorated, a higher proportion of the continental waterfowl production is coming from northern production areas. With the deltas of the Saskatchewan, Mackenzie and Yukon rivers, the Peace-Athabasca Delta is extremely important for continental waterfowl populations (Hennan 1973). Whether these conclusions will remain valid in the wake of the W.A.C. Bennett dam and remedial weirs is not known.

Waterfowl harvested by the residents of Fort Chipewyan are eaten fresh in spring and summer but are frozen and stored in fall. Gathering of waterfowl eggs was widely practiced by native people until fairly recent times, but is no longer common anywhere in the Mackenzie River Basin (Hennan 1973, Barry 1973).

b. Slave Delta:

Reconnaissance surveys of waterfowl on the Slave Delta in the past (Soper 1952, 1957) concluded that it was important to waterfowl but on a unit area basis not as important as either the Peace-Athabasca or the Mackenzie deltas. Recent work, which spanned only a single year (Thompson et al. 1979), forms the basis of the following discussion.

In both spring and fall, the Slave Delta appears to be an important subunit of a larger staging area which extends east from the delta along the south shore of Great Slave Lake through a series of shallow bays to the mouth of the Taltson River. The entire area appears to be particularly important to geese and whistling swans and was considered by Thompson and co-workers (1979) to be of comparable value to the Mills Lake-Beaver Lake area, discussed later.

As in other deltas of the basin, breakup and flooding of the Slave Delta occur earlier than in adjacent areas. Early melting on the delta also contributes to the early formation of shoreline leads along Great Slave Lake. Early migrating dabbling ducks are attracted to the delta by the open water. Large mudflats formed by sediment deposited in spring are exposed by receding water levels late in summer and are used by fall migrants. Early successional plant species such as horsetail provide food for migrating geese and ducks, particularly in fall (Thompson et al. 1979).

Breeding densities of waterfowl on the Slave Delta were relatively uniform throughout the entire area. However, dabblers tended to be more common in newer parts of the delta, near the lake, while divers were more prevalent on more stable, interior ponds (Thompson et al. 1979).

Breeding pair densities observed on the Slave Delta were comparable to those observed on the Peace-Athabasca Delta (Thompson et al. 1979). However, to be truly comparative, surveys should be done in the same year. Many factors influence the size and proportions of the populations of waterfowl that travel north in any year. In addition, water levels on a northern staging area may affect its level of use. When data were collected on the Peace-Athabasca Delta (1971-1976) water levels were regulated.

The Slave Delta is superior to the surrounding boreal forest for waterfowl production because it offers

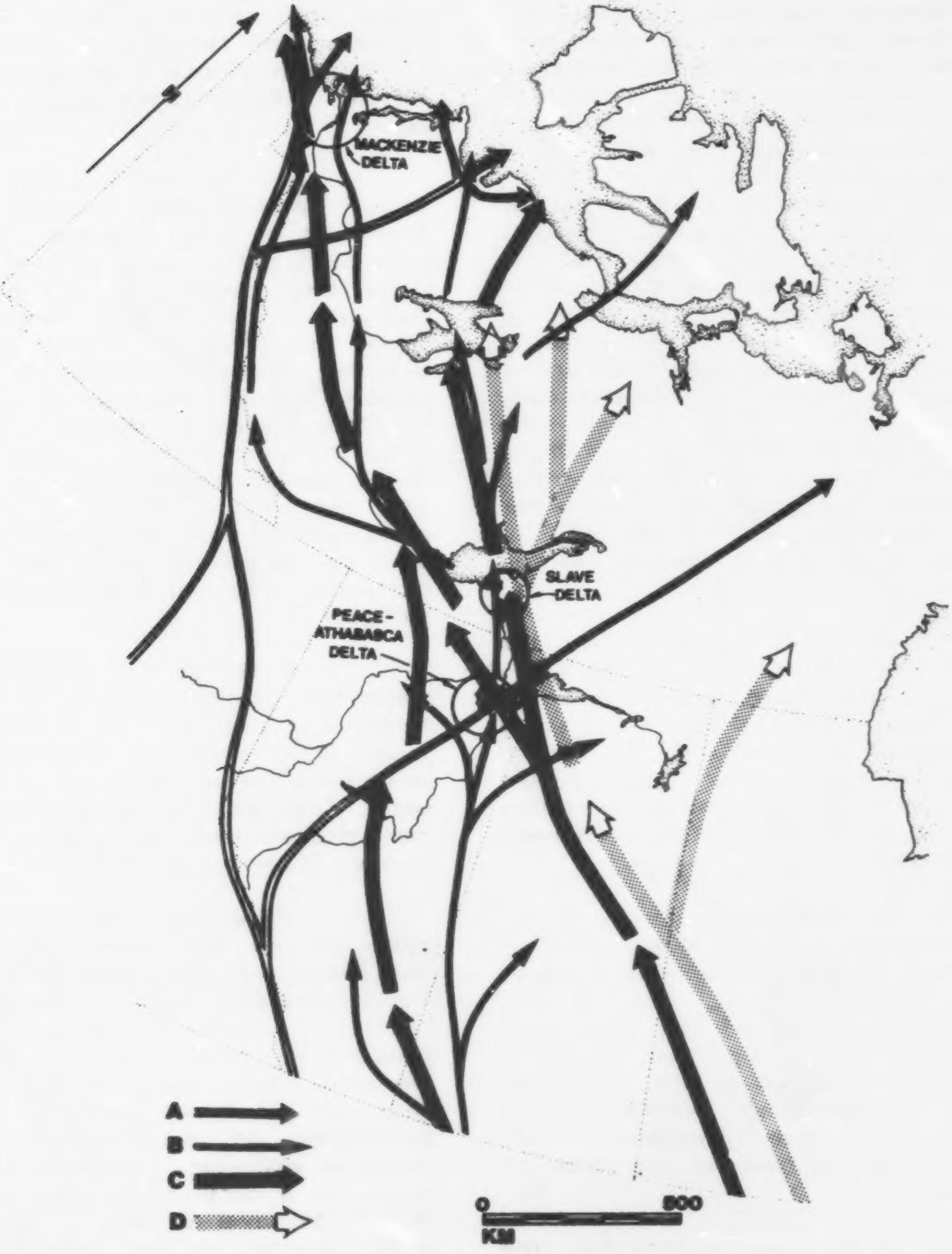
MACKENZIE DELTA
SLAVE DELTA
PEACE-ATHABASCA DELTA
A
B
C
D
0
800
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Figure 32. FLYWAYS OF MIGRATORY WATERFOWL IN THE MACKENZIE RIVER BASIN
A. Pacific flyway; B. Central flyway; C. Mississippi flyway; D. Atlantic flyway (adapted from The Peace Athabasca Delta Project Group 1972)

more diverse and attractive habitats. Preferred habitats are maintained by flooding and sedimentation. Perched basins and oxbow lakes would become overgrown with vegetation if not periodically recharged with water (Thompson et al. 1979).

Apart from waterfowl, the Slave and other deltas provide summer habitat for a varied fauna of migratory birds, many of which are not found in adjacent boreal uplands. On the Slave Delta, bird species other than waterfowl were studied. Large flights of shorebirds, largely pectoral, semipalmated, and Baird's sandpipers occupied silt flats and sandspits during fall migration. Colonies of arctic terns and California gulls were found on sandspits and nests of black terns occurred in the horsetail fringe bordering several lakes (Thompson et al. 1979).

c. Mackenzie Delta: Millions of birds, representing 139 species, are found in the Mackenzie Delta-Beaufort Sea region. The Mackenzie Delta is an important area for waterfowl. Large numbers of swans, geese, ducks, gulls, terns, and other species converge on the Mackenzie Delta each spring. On their semi-annual migrations they travel between the delta and wintering areas as far south as South America and Antarctica (Berger 1977). Most arrive on the delta between early May and late June. For many species the delta is a very short spring stopover enroute to nesting areas further north, east and west. Open water which appears earlier on the delta than in adjacent areas at similar latitudes attracts the early migrants.

The most dramatic concentration of waterfowl on the Mackenzie Delta occurs in fall, when large numbers of ducks, geese and swans aggregate on the delta to feed and rest prior to their long flights south. Although birds arrive on the nesting ground in spring in top physical condition, incubation and moulting require more energy than can be supplied by their summer feeding. Prior to heading south, some northern bird species take a short hop from their nesting grounds to areas such as the delta where there are extensive food resources. The early staging period of 2 to 4 weeks is particularly important for building fat reserves. Patterson (1974) reported body weights of lesser snow geese that stage on the north slope and the delta to increase 9.5% to 23% during the early staging period in one year. If geese or ducks begin to migrate in poor condition they must rest more frequently on the journey south and thereby become more vulnerable to hunters (Patterson 1974).

The area around Shallow Bay is particuarly noted as a fall staging site for ducks and geese. The entire western Canadian arctic population of lesser snow geese stages on the north slope of Yukon and Alaska or on the Mackenzie Delta in numbers as high as 400 000 in some years (Koski and Gollop 1974). The delta is most important to lesser snow geese in years when snow and freezing temperatures come early to the north slope. White-fronted geese, Canada geese, black brant, whistling swans, and a variety of ducks are also present on the outer delta (Koski 1977). Many ducks also stage in Shallow Bay (Searing et al. 1975) and in the Main Channel (Poston et al. 1973) in fall. T. Barry, Canadian Wildlife Service (cited by Allison 1977) considered a coastal zone of the delta about 25 km wide to be more important to migratory birds than interior areas.

In the interior Mackenzie Delta, "reverse deltas" (Gill 1974) project into some lakes. Those geomorphic features are favored resting spots for staging ducks in fall because they offer good visibiliby and protection from terrestrial predators. They are also the only locations in the delta that support stands of **Beckmannia syzigachne**, the seeds of which are eagerly eaten by ducks. Gill (1974) hypothesized that this grass is maintained in the area by seeds carried and deposited by ducks moving into the area from the south.

Four islands in the Kendall Island Migratory Bird Sanctuary, on the outer Mackenzie Delta, are the nesting area of the smallest lesser snow goose colony in the western Arctic. The islands are largely sedge-covered. Levees formed by ice pressure during break-up and entrapment of silt provide the driest locations for nesting. In recent years, the nesting colony of 400 to 500 adult lesser snow geese has been almost totally unsuccessful (T. Barry, Canadian Wildlife Service, cited by Allison 1977). Apparently in 1978 nesting and brood raising were successful for the first time in nine years. The 1979 and 1980 seasons again resulted in little production (A. Goodman, Canadian Wildlife Service, pers. comm.).

It is not known to what extent activities of man are responsible for the poor breeding record of the Kendall Island lesser snow goose colony. Adverse weather conditions or disturbance by barren ground grizzly bears and other predators may account for losses of nests and/or young of up to 100% in some years. Martel (1976) commented that waterfowl populations may be more sensitive to disturbance in years of stormy, cold weather because of the poor physiological condition of the birds. The Kendall Island colony has been unsuccessful while other western lesser snow goose nesting colonies have flourished. During the same period, it has been subjected to disturbance from oil exploration activities.

The outer Mackenzie Delta is an important nesting area for whistling swans. Although swan nests are well spaced along the shores of tundra ponds, densities of nesting swans in the western part of the delta are the highest ever recorded (T. Barry, Canadian Wildlife Service, pers. comm. cited by Allison 1977). That population is an estimated 20 000 birds (Campbell and Weber 1973, Bellrose 1976). The Harry Channel and Swan Channel regions to the east of the Kendall Island sanctuary are critical habitat for nesting and moulting waterfowl, including whistling swans, white-fronted geese, sandhill cranes and various shorebirds (Barry 1976).

The delta also supports several species of nesting ducks. Among the dabbling ducks, pintail and mallard are most common; greater scaup, and surf scoter represent the divers (Searing et al. 1975). Breeding indices of 80 000 to 335 000 nesting ducks were recorded (Smith et al. 1964). Flooding of the delta in spring, flooding in conjunction with high tides, and storm surges during the nesting season may drown the nests of many species of waterfowl and reduce waterfowl production. Like the Peace-Athabasca Delta, the Mackenzie Delta supports the highest concentrations of waterfowl during years of drought on the prairies.

The rare Hudsonian godwit, a shorebird, is found in relatively concentrated numbers in the delta (McTaggart-Cowan 1976). Other shorebirds of various species are also a major component of the avifauna of the delta. Some raptors nest in the Mackenzie Delta. Rough-legged hawks are found in the outer delta, particularly Richards Island. Bald eagles reach the northern limit of their inland range when they nest on the delta. Merlins are found in specific areas of the delta (Searing et al. 1975), and peregrine falcons occur in the Campbell Hills near Inuvik.

Large numbers of sandhill cranes migrate through the delta and a few nest along the coast.

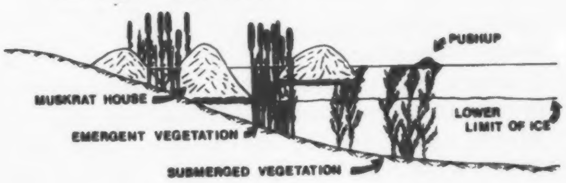
Migratory waterfowl are hunted by native people on all of the major deltas in spring, summer, and fall. In northern areas, spring birds are particularly welcome because they provide a change in diet and because they are fat. Geese and larger ducks are favoured in the hunt. Hunting occurs on the deltas throughout the open water season, often in conjunction with other activities. Gill (1973b) remarked that reverse deltas in certain lakes of the Mackenzie Delta are among the hunting sites chosen by native people because of their attraction to waterfowl. Barry (1973) pointed out that the spring hunt is a social and cultural event as well as representing a change in diet and activity after a long winter.

2. Aquatic Furbearers: Muskrat and beaver, particularly the former, have been staples of the northern fur trade since it began. The concentrations of wetlands and fluctuating water levels in the deltas combine to provide some of the best muskrat habitat available in the Mackenzie River Basin.

Like waterfowl, muskrats depend on fluctuating water levels to produce and maintain optimum habitat. For instance, seeds of some species of emergents favoured for food and house construction, such as bulrush, cat-tail, sweetflag, and bur-reed, will only germinate on exposed mudflats (Ambrock and Allison 1973). Like waterfowl, muskrats have a greater reproductive success in years when water levels are fairly stable. Summer floods may drown helpless young in bank burrows or houses, and severe recessions expose bank dens and even houses to predation. In contrast to waterfowl concentrations, however, muskrats appear to thrive when water levels are relatively high (Ambrock and Allison 1973).

In northern areas, fall water levels at bank dens or houses and severity of the winter affect survival of muskrats over winter. Although muskrats may survive in locations which do not retain water under the ice, their opportunities are better if they can swim to food, whether it is submerged or emergent plants. Offsetting the danger of freezing out (Figure 33) is the fact that neither emergent nor submerged plants usable by muskrats are available in deep water. The habits and habitat of muskrats, then, force them to live in water-edge locations which must periodically suffer recessions and floods to maintain appropriate plant communities. Both recessions and floods can have direct negative consequences for muskrat populations.

A. High water level



B. Low water level

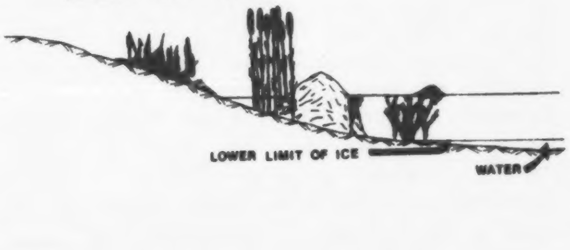


Figure 33. INFLUENCE OF WATER LEVELS ON WINTER SURVIVAL OF MUSKRAT

Under relatively high water levels, when extensive stands of emergent vegetation are flooded, many sites are available for the building of muskrat houses. Emergent and submerged vegetation remains available under the ice for food. A relatively high proportion of the muskrat population will probably survive the winter. In contrast, when water levels are lowered, fewer suitable sites are available for building houses. Availability of food is severely reduced when no water remains under the ice sheet in the zones occupied by emergent and submerged vegetation. A relatively low proportion of the muskrat population is likely to survive the winter (Figure 33). A similar relationship between water levels and overwinter survival occurs where muskrats inhabit bank dens.

a. Peace-Athabasca Delta: Although a 10-year abundance cycle has been postulated for muskrats (Fuller 1951), it appears that water levels and the changes in habitat caused by them play an important role in regulating muskrat populations throughout their worldwide range (Bellrose and Brown 1941, Chesnokov 1971). On the Peace-Athabasca Delta, early fur traders were the first to record that muskrat populations tended to be low when water levels were low, and high when water levels were high (Wuetherick 1973).

Muskrats on the Peace-Athabasca Delta live either in houses built of emergent vegetation or in bank dens (Ambrock and Allison 1973). Building of houses requires an abundant supply of emergents which are also a primary source of summer food, while bank dens can only be built on steep banks beside deeper water. Adult females on most delta lakes produce two litters each year. However, in some areas, three litters were found (Ambrock and Allison 1973).

Winter survival of muskrats is directly related to fall water depths at the house or den site. At sites that freeze to the bottom, muskrat survival was lower than at sites where water was present all year. Minimum depths required for optimum survival were determined to be 0.75 m in 1971 and 0.6 m in 1972. In 1972, 70% of the delta lakes did not fulfill that requirement (Ambrock and Allison 1973). Under some conditions, winter muskrat houses on the Peace-Athabasca Delta may themselves be a source of food for muskrats. Westworth (1974) examined used houses in spring and found them to be only thin shells.

High water levels in the delta since 1972 after the Quatre Fourches weir and the Riviere des Rochers dam were constructed resulted in rapid colonization by muskrat of newly available habitat (Stelfox and McGillis 1977).

Muskrat populations on most of the delta were at extremely low levels in 1971 (Ambrock and Allison 1973), although reduced survival capacity because of low water resulted in no observations of starvation, emigration, disease, or intraspecific competition (Westworth 1974). When water levels increased, the muskrat population also increased. The complex effects of the Peace and Athabasca rivers on water levels of the delta and the complicating addition of weirs resulted in an asynchrony of increase and decrease in muskrat populations in different delta sectors. The delta-wide effect was to spread the peak of abundance over the four years 1973-1976. In some areas, populations increased 500% in three years. In 1976, despite continuing control of water levels, muskrat numbers declined throughout the delta (Poll and Stelfox 1978a). Declines occurred largely because of habitat loss.

The weirs have resulted in prolonged flooding of open basins during the growing season and have failed to recharge perched basins. In perched basins that are not flooded, plant succession is eliminating muskrat habitat. In open basins that are flooded, reed-swamp vegetation is stagnating and degenerating; reproduction of some emergent species of plants is inhibited, and others become deficient in nutrients required by muskrats. Muskrat habitat is being eliminated in those areas also (Poll and Stelfox 1978a, 1978b). A habitat analysis in 1978-79 showed that preferred emergent communities of reed grass, giant bur-reed, horsetail, bulrush, and cat-tail (with a combined area of 19% of the total area mapped) contained 83% of the total number of houses found (Poll 1980). Periodic floods and recessions are required on a three to five year basis to maintain optimum conditions for muskrats (Poll and Stelfox 1978a, 1978b).

Reduction in available habitat is considered to be a major contributor to declines in muskrat populations (Poll 1980). However, heavy trapping pressure may have accentuated declines. In the Wood Buffalo Park portion of the delta alone, muskrat fur harvests increased 3 400% from 1971-72 to 1976-77 (Stelfox and McGillis 1977). The increase in trapping effort coincided with an increase in populations of muskrats, but harvests increased at a greater rate than did numbers of muskrats.

b. Slave Delta: On the delta of the Slave River, muskrat populations are more successful in channels than in the few lakes (Law 1950, Geddes 1980). While Law (1950) failed to find any houses, Geddes (1980) did, although none of them supported muskrats during winter. Because the lakes are shallow and have a gentle slope, they are unsuitable for bank dens, unlike many lakes in the Mackenzie Delta (Geddes 1980). Law (1950) commented that muskrats were not found in channel banks subject to ice abrasion, wind or current erosion, or heavy silt deposition. Most channels do not freeze to the bottom in winter and support growths of horsetail sufficient to support muskrats in winter. Geddes (1980) indicated that during normal winter water recessions, muskrats may forage under the hanging ice along the channel bank (Figure 34), although such behaviour makes them vulnerable to predation from mink which may also be found in those areas (Stevens 1953) in all three deltas.

c. Mackenzie Delta: The muskrat is a mammal of major economic importance in the Mackenzie Delta area. The inner delta as far north as treeline is excellent muskrat habitat. The only other section of the Mackenzie River Basin north of 60° N which may equal it is the Brackett Lake wetland (Dennington et al. 1973). Muskrats are

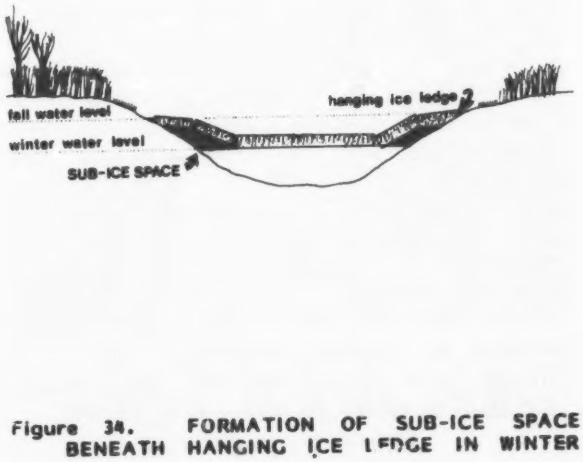


Figure 34. FORMATION OF SUB-ICE SPACE BENEATH HANGING ICE LEDGE IN WINTER

present in most permanent bodies of standing water. Optimum water depth for winter survival is 2 m (Stevens 1953). Since deep lakes do not produce appropriate vegetation for muskrat food and since ice has an average thickness of 0.75 m in the Mackenzie Delta, muskrats have a narrow range of lakes in which to live. Unlike muskrats of the Peace-Athabasca Delta, most of which build houses of emergent vegetation, the populations in the Mackenzie Delta are restricted to bank dens. Muskrats throughout the north build pushups to extend their effective foraging range. Pushups are mounds, usually of submerged vegetation, pushed up onto the surface of forming ice in fall. During winter the muskrat has a protected air space above the ice to use as a feeding platform.

Because muskrats are prolific and colonize new habitats quickly, temporary disturbance of small areas of their habitat will have only temporary effects on populations. In the Mackenzie Delta, dispersal takes place largely after break-up, and virtually all suitable summer habitat is then occupied. In winter, many muskrats move back to deeper lakes for wintering (Westworth and EPEC Consulting Western Ltd. 1977). During winter, too, mortality may be as high as 50% of the annual increment (Hawley and Hawley 1975). Females may produce two litters per year, although the frequency with which they do so is unknown (Stevens 1953). Mackenzie Delta muskrats may be smaller than more southerly members of the same race because limited availability and poor quality of food does not allow them to develop their full potential for growth (Westworth and EPEC Consulting Western Ltd. 1977). However, stabilization of muskrat habitat or long-term declines in water levels on the Mackenzie Delta could result in serious declines similar to those that occurred on the Peace-Athabasca Delta in the early 1970's.

Muskrats are present on Richards Island but the remainder of the outer delta is unsatisfactory habitat and is sparsely populated. During the open water season, the shallower lakes of the outer delta experience greater fluctuations in water level than do lakes further inland. Apart from normal spring floods, young muskrats on the outer delta are at risk of drowning when onshore winds or storm surges inundate the area. As water recedes, bank burrows may be uncovered and therefore become vulnerable to invasion by predators. Frequent flooding also accelerates siltation to the detriment of muskrats (Stevens 1953).

Particularly in late spring, pushups of muskrats on the outer delta and Pleistocene Mackenzie Delta are susceptible to destruction by predators. Foxes and grizzly bears are known to open muskrat pushups. In spring, nearly all bears observed on Richards Island systematically searched lakes for pushups which were torn apart and the vegetation eaten. Frozen muskrats and freshwater snails may also be available to the bears. Reindeer and sandhill cranes also eat muskrat pushups (F.F. Slaney and Company Limited 1974).

Chesnokov (1971) summarized the effects of floodplain flooding and drawdowns on muskrats. This Russian work indicated that although high and prolonged floods, and the recurrence of low and short floods, both lead to reduction in numbers of muskrats, the mode of action is different. High and prolonged floods cause direct death of the animals, prevent breeding, and reduce the food supply while low floods of short duration reduce the area of suitable habitat and have an adverse general effect on habitat characteristics.

Virtually all muskrat hunting and trapping from communities near deltas occurs directly on the deltas. Although some trapping is done under the ice in late fall and early winter, the preferred and most efficient technique is hunting from a canoe during spring break-up. Hunting of muskrats in good habitat provides a guaranteed cash return for effort expended over a short period of time. It shares with waterfowl hunting the cultural importance of spring activities on the land. Hunting terminates prior to production of the earliest muskrat litters.

Hunting effort and catches of muskrats vary to some extent with muskrat population and fur price. The best documented example from the recent past occurred on the Peace-Athabasca Delta. From low harvests of 2 000 in 1971-72 on the Wood Buffalo National Park part of the delta, the harvest increased to 67 964 in 1976-77 as the muskrat population increased. Total harvest on the delta in 1976-77 was 156 769 (Poll and Stelfox 1978a, 1978b), the highest estimate recorded for the area. On the Mackenzie Delta, all lakes and many channels in the upper and middle delta have been exploited for muskrat at some time (Usher 1976). Muskrats are an important food source for trappers and hunters in spring. Many animals taken for fur are boiled and eaten.

Considering all three deltas in the Mackenzie River Basin, good habitat for beaver is found only in the inner Mackenzie Delta, although some of the least active parts of the Peace-Athabasca Delta also support beaver. Beaver populations in Wood Buffalo National Park are highest in non-alluvial, non-delta areas in the northern part of the park (Novakowski 1958).

The history of beaver on the Mackenzie Delta has been strongly influenced by trapping. Declines from relatively high numbers to low populations were attributed to heavy trapping pressure, particularly after beaver populations recovered under protection of the Mackenzie Beaver Sanctuary. More recent declines have been found to be associated with degradation of food supplies over time, which suggests that over-trapping may not have been responsible for historic declines (Hawley and Aleksiuk 1973).

When populations were high, densities of 0.75 beaver colonies per square mile (0.29/km^2) were recorded in parts of the Mackenzie Delta. Most beaver in the delta use bank burrows, and are found in lakes rather than channels because channels are subject to unstable water levels. Preferred habitats for beaver in the delta are areas of poplar and willow. Poplar grows into meander scroll depressions (Figure 35) which retain surface runoff and become attractive to beaver (Gill 1972b). Overuse of habitat occurs

Figure 35. MEANDER SCROLL DEPRESSIONS SUPPORT STANDS OF POPLAR WHICH ARE ATTRACTIVE TO BEAVER (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

frequently and colonies may move every one or two years (Hawley and Aleksiuk 1973).

3. Ungulates: Although moose are important to the economies of communities near all three deltas, they do not play a major role in delta ecology. Moose habitat on deltas occurs largely in more stable areas where tall shrubs, deciduous trees and conifers are present.

a. Peace-Athabasca Delta: Several locations on the margin of the Peace-Athabasca Delta carry relatively high densities of moose during winter. Numbers of moose have remained lower than the area can support, partly because of heavy hunting pressure (Allison 1973a).

The Peace-Athabasca Delta is the only one of the three deltas in the basin that supports bison. Although the hybrid wood bison-plains bison is found throughout Wood Buffalo National Park, highest numbers and largest herds usually occupy the open grasslands of the delta.

Bison are mainly grazers and depend primarily on the extensive sedge meadows of the delta, although reedgrass is also eaten. In spring, some stands of horsetail are entirely eaten (Allison 1973b). During spring and summer, bison concentrate on the extensive Sweetgrass Meadows where calving occurs. In winter they move from large open meadows into smaller sheltered sloughs, although sedges and reedgrass remain their major foods (Allison 1973b).

Drowning has been a major cause of bison mortality during years of high water on the delta (Soper 1941, Fuller 1966). Most drownings occur during spring floods but some animals apparently fall through melting ice prior to break-up. Numbers of animals drowned each year are probably a function of area of delta flooded, duration of the flood, characteristics and timing of break-up, and variation in bison movement patterns (Allison 1973b). Soper (1941) estimated that 30 to 40 animals per year died in floods. However in 1961, 1 000 to 3 000 animals may have died (A. Campbell, Fort Chipewyan, pers. comm. cited by Allison 1973b), and high water on the delta in 1974 drowned 2 000 to 3 000 bison and reduced their range (Oosenbrug et al. 1980).

Although bison occur in greatest numbers on the delta, they are found throughout Wood Buffalo National Park. Total numbers of bison in the park have fluctuated widely since the first counts in 1934. Estimates have been as low as 5 500 to 6 000 animals and as high as 12 000 to 15 000 (Stelfox 1977, Allison 1973b). Numbers of bison using the delta have dropped substantially since 1971-72, severe mortality was caused by drowning, and water levels on the delta since 1974 have limited the quality and availability of bison habitat (Cordes 1975).

Collingwood (1977) outlined habitat types chosen by bison in Wood Buffalo National Park (Table 3). Although all bison observed in the park were not necessarily found in alluvial locations, the choice of dry grassland and wet grassland locations in all seasons indicates the importance of those successional phases to bison.

Low water levels on the delta provide a short term benefit to bison as new areas of sedge and meadow are established. However on the Peace-Athabasca Delta, sedges are the favored food of bison and require a wet environment. The wet meadows are periodically inundated by water Surface water is present seasonally, but the water table remains in the rooting zone of the plants during at least part of the growing season. If

TABLE 3. BISON SEASONAL DISTRIBUTION AND HABITAT USE IN WOOD BUFFALO NATIONAL PARK.*

	May 76	Sept 76	Nov 76	Mar 77	May 77
Percent of bison observed in various locations					
Delta floodplain	54.0	58.1	57.9	63.1	62.2
Upland Boreal Forest	33.4	19.1	15.2	12.8	27.0
Salt Plain	7.2	22.5	17.1	24.1	5.1
Slave River Lowlands	5.5	0.3	9.8	0.0	5.7
Percent of bison in various habitat types					
Dry Grassland	81.6	85.8	73.4	69.9	36.6
Wet Grassland	16.9	12.5	21.2	22.2	19.2
Riparian	0.4	0.2	1.9	0.0	0.4
Scrubland	0.1	0.0	3.2	6.9	39.4
Forest Land	1.0	1.5	0.3	1.0	4.5

* From Collingwood, L. (1977).

water levels remained low or stabilized, sedge meadows would deteriorate in quality (Allison 1973b) as plant species better adapted to drier environments invaded and gradually succeeded the sedge.

High water levels and prolonged flooding of the sedge and reedgrass meadows occurred after the building of the Quatre Fourches weir. Flooding in 1972 and 1973 eliminated more than one half of the sedge meadows and two thirds of the reedgrass meadows. Sedge and reed-grass were replaced by whitetop and open water. Remaining wet meadows often exhibited low vigor (Cordes 1975).

The sedge and reedgrass meadows which occurred on the Peace-Athabasca Delta were the result of temporary early summer flooding under the natural hydrologic regime of the area. They are intolerant both of drying (Allison 1973b) and of permanent or prolonged late summer flooding (Cordes 1975). It is evident that prolonged flooding and high water levels severely reduced both habitat and food available to bison on the delta. Placement of weirs on the delta has not approximated the natural hydrological regime and seems to have reduced and damaged bison ranges south of the Peace River.

b. Mackenzie Delta: The Mackenzie Delta is poor moose habitat. Although food species are plentiful, the delta is limited in value by frequent flooding and lack of protection from wind (Prescott et al. 1973). In addition, moose are almost always shot when encountered in the Mackenzie Delta by native travellers.

4. Marine Mammals: Of the three major deltas in the Mackenzie River Basin, only the Mackenzie Delta is marine. White whales are the only marine mammal to occur in large numbers within the zone of influence of the Mackenzie River. These whales are temporary summer visitors to estuarine areas. About the end of June, after break-up, 4 000 to 5 000 whales move into the turbid Mackenzie River estuary. The whales are believed to be attracted to the estuary by the warm (up to 15° C) water which they may require for calving. Little feeding occurs in the estuary (Fraker 1978). Peak numbers occur in late July, but many whales remain in the vicinity until mid-August. That group of whales is the only population of white whales in the western Arctic. Although the function of the estuary in the life history of white whales is not completely understood, the area is believed to be critical to survival of the population. No alternative habitat of equivalent size is found elsewhere in the western Arctic (Sergeant 1976, Fraker 1978).

The annual whale hunt is an important early summer event on the Mackenze Delta. Whole families of

Inuit move to camps in the outer delta to fish, camp and hunt whales. The harvest is relatively consistent from year to year and provides a supply of muktuk for delta communities.

B. Wildlife and Wildlife Habitat of Non-deltaic Alluvial Areas

1. Birds: Some migratory waterfowl tend to follow watercourses during migration. River valleys are used by a variety of species for short rest periods during spring because the rivers have patches of open water earlier than nearby lakes. Leads around islands and along shores open early and pools of water may appear where tributaries meet a main river channel. Numbers of birds using such areas are relatively low in comparison with deltas. For instance, Bernard and Kemper (1976) stated that the main river and tributary valleys of the Peace River are not heavily used by either migrating or breeding waterfowl. Nevertheless, break-up along the Mackenzie River and its tributaries does provide significant spring staging habitat. Of particular importance is the fact that pairing and mating of some species may take place during the spring flight. Although few locations at which this occurs are known, lesser snow geese pair and mate on the Mackenzie River Islands near Norman Wells (Poston et al. 1973).

Most parts of river valleys are less important to migrating waterfowl in fall than in spring (Bernard and Kemper 1976). During fall flights, water is available elsewhere and birds tend to use lakes with abundant food resources.

Important staging areas usually provide a mixture of marsh vegetation and mudflats in areas subject to variable flows of water, similar to deltas. Examples of suitable staging habitat include: the west end of Lesser Slave Lake, a small delta area; the Hay-Zama Lakes wetland, a broadened floodplain of the Hay River; and the Mills Lake region, a floodplain of the Mackenzie River. These staging habitats within the basin host large numbers of ducks, geese, and swans (Weaver 1970, Weaver 1971, Kemper et al. 1975).

River channels are not generally suitable for nesting waterfowl. On the Peace River, dabbling ducks were usually associated with backwater channels or islands during breeding and brood rearing; diving ducks were seen along the river channel itself, although both occurred in small numbers. Ice jams, scour, and flooding maintain areas of silt, gravel or cobble along rivers which support scanty, hardy vegetation of certain willows, sedges, rushes and forbs. A few species such as Canada geese nest and graze along ice-scoured river edges (Bernard and Kemper 1976). However, considering the entire Mackenzie River Basin, suitable marshes provide most waterfowl production. The west end of Lesser Slave Lake and the Hay-Zama Lakes have some of the best waterfowl production habitat in the region (Weaver 1970, 1971).

Populations of migratory birds other than waterfowl have not been studied in much detail in the Mackenzie River Basin. However, present knowledge indicates that deciduous vegetation supports a greater diversity of birds than do plant communities which are predominantly spruce. The greater number of species seems to be related to the structural complexity of available habitat. For instance, a single species may require one type of habitat for nesting, a second for territorial display, and a third for foraging (Salter and Davis 1974). Alluvial plant communities supply the required diversity of habitat types to support a variety of species, but total number of species present generally declines with increasing latitude. However, there is no statistical correlation between total density of birds and latitude (Salter and Davis 1974). Along the Mackenzie River valley, Tull et al. (1974) found the greatest number of species and the highest index of density in spruce-Sphagnum muskeg. Most studies (Salter and Davis 1974, Tull et al. 1974) separate habitats on the basis of plant community rather than origin of parent material. Because alluvial sites support several plant communities, in total they probably host the greatest variety of terrestrial bird species.

The Athabasca River valley contains an abundance of favourable habitats for terrestrial migratory birds - more than adjacent uplands. By implication, the river valley is more important for terrestrial migratory species than the uplands are; more than 100 species breed in the river valley in the Fort McMurray area where diversity of feeding and resting areas is provided by the variety of tree and shrub species, the variable vegetation heights and densities, and the abundance of edges between habitat types (Smith 1979).

Along the Peace River, alluvial sites support a variety of plant communities. The more important features influencing plant communities are considered to be slope, aspect, soil and soil moisture. The presence of non-alluvial topographic features such as cliffs along many rivers also influences distribution of birds in alluvial areas (Bernard and Kemper 1976).

Balsam poplar forests along the upper Peace River have a heavy understory of shrubs. Yellow warbler and red-eyed vireo were species often seen in that habitat, and the American kestrel, common goldeneye, common flicker and bufflehead all nest in balsam poplar trees. The mixed balsam poplar-white spruce forest was extensively used by a variety of passerines including Swainson's thrush, red-eyed vireo, yellow warbler, least flycatcher and American redstart. The species that nest in poplar trees were again found in poplar in the balsam poplar-white spruce forests. In addition, merlins nested in spruce trees, particularly at locations where white spruce formed a fringe between cliffs and the river (Bernard and Kemper 1976).

The mixed birch-spruce forest was found mainly on better drained slopes along tributary streams. It supported the greatest variety of passerine species, including the clay-coloured sparrow, least flycatcher, chipping sparrow, red-eyed vireo, magnolia warbler and black-throated green warbler. In aspen stands least flycatcher, red-eyed vireo, hermit thrush, robin, yellow warbler and Swainson's thrush were most common (Bernard and Kemper 1976).

Non-migratory game birds that use alluvial areas along rivers include grouse and ptarmigan. In southern parts of the basin, ruffed grouse are common in deciduous and mixed forests, many of which occur on alluvial terraces. Ruffed grouse remain in similar home ranges all year long. Further north in the basin, willow ptarmigan are common in alluvial sites (Figure 36). In winter, ptarmigan flock to appropriate semi-open habitat in groups of up to several hundred. Their requirements seem to include willows with buds that protrude above the snow for feeding, taller willow for cover, and open areas with relatively deep soft snow for burrowing (F.F. Slaney and Company Limited 1974). That combination of habitat requirements is often found on alluvial sites along aggrading banks.

Figure 36. WILLOW PTARMIGAN OFTEN USE ALLUVIAL SITES WHERE WILLOW IS PLENTIFUL IN WINTER AND SPRING (Courtesy of L.M. Allison, Salix Enterprises Ltd., Cowley, Alberta)

The non-migratory game bird taken in largest numbers in the Mackenzie River Basin is probably willow ptarmigan. During winter when the birds are flocking in alluvial sites they are often hunted in locations from Fort McMurray north.

2. Aquatic Furbearers: Muskrats occur along river channels, but in swiftly flowing water they are found only in low densities. Beaver are better adapted than muskrats to river channels and deeper lakes. In swiftly-flowing water they usually construct bank dens although lodges are found. Beaver forage for food in older alluvial sites that support willow, balsam poplar, and alder. In southern parts of the Mackenzie River Basin, their food supply includes birch and aspen.

In northern parts of the basin particularly, a shortage of food may limit the period of time a beaver colony can occupy certain sites (Hawley and Aleksiuk 1973), while colonies at other locations seem to remain indefinitely (Novakowski 1967). Further south, parts of the Peace River below the W.A.C. Bennett Dam no longer freeze in winter. Some of the beaver inhabiting these areas apparently do not build food caches but rather forage for food all winter (Blood 1979). Along rivers continual destruction and building of alluvial habitats perpetuate conditions which maintain a food supply for beaver.

Beaver populations in the Mackenzie River Basin fluctuated widely in the past and in several areas harvesting was prohibited to allow populations to recover. Although the Kakisa River drainage supports the highest recorded densities of beaver in the Northwest Territories (Fuller 1953, Novakowski 1967), bog areas seem more important to beaver than alluvial or mountain regions. Water in bog areas moves relatively slowly and can be readily controlled by beaver (Wooley 1974).

3. Terrestrial Furbearers: Many furbearers are found within alluvial plant communities. Even marten, traditionally considered a species of pure conifer stands, occur along upland river valleys and terraces where densities of their prey are high (Wooley 1974). Lynx may also be found in the mixed coniferous and deciduous forests of river terraces (van Zyll de Jong 1963) when snowshoe hare, their principal prey, are present. Along the Athabasca River near Fort McMurray, D.A. Westworth and Associates (1979) reported that coyote populations fluctuate in response to populations of snowshoe hare.

Wolves occur throughout the Mackenzie River Basin in association with populations of ungulates. Where moose or bison concentrate in alluvial areas, wolves are sure to be present unless competition with man has removed them.

Red squirrels occur near Fort McMurray in coniferous and mixed-wood habitats, but exhibit a strong preference for white spruce (D.A. Westworth and Associates 1979) which is normally found in alluvial areas.

Grizzly bears in the Mackenzie Mountains and Rocky Mountains use broad areas of varied habitat throughout the year, and are largely herbivorous. Vegetation in the gravel along braided reaches of tundra rivers is often virtually plowed every spring by bears eating sweet vetch roots (Figure 37). Later in the season, alluvial sites are also popular with bears for the crops of berries on their gravel bars, particularly soapberry (Pearson 1975).

Black bears are known to winter in concentrations of dens on certain islands in the Liard River (S. Miller, Northwest Territories Wildlife Service, cited by Donaldson and Fleck 1980). Unfortunately, there are no data available on physical or vegetational features of the islands or the extent of use by bears. It is not known whether islands in other parts of the Mackenzie River Basin are important sites for denning black bears.

Near Fort McMurray and Cold Lake, black bears exhibit a preference for aspen and mixedwood habitats. The food species most heavily used by black bears during spring and summer are vetchling and sarsaparilla found in the understory of aspen stands. The black bears avoid large openings where food is unavailable (Young 1978). Although not exclusive to alluvial sites, aspen and mixedwood habitats suitable for black bear are often found on river terraces.

4. Ungulates: Moose are a staple of the northern economy and are widely recognized as a species which depends on early succession plant communities for food, particularly in winter. Alluvial communities along

Figure 37. GRIZZLY BEAR WITH CUBS FORAGING ON A BRAIDED STREAM BED WHICH HAS SUCCEEDED TO SWEET VETCH AND SOAPBERRY (Courtesy of L.M. Allison, Salix Enterprises Ltd., Cowley, Alberta)

river channels and minor deltas provide optimum winter habitat for moose (Figure 38).

Moose, like other northern ungulates, subsist through winter in a state of negative energy balance (Dickinson and Herman 1979). That is, they do not eat enough food to maintain their body weight. Alluvial plant communities provide suitable food species for moose in association with nearby stands of conifers which are used as cover. Islands are particularly favoured wintering sites for moose in the Mackenzie River valley (Walton-Rankin 1977). Further south, along the Peace River, Blood (1979) recorded highest numbers of moose in river valleys during winter, but heaviest use of islands later in spring by female moose with calves. He commented that the importance of islands for calving is not known. Near Fort McMurray major moose wintering areas are seral forests containing an abundance of shrubs and deciduous trees interspersed with stands of coniferous cover, mainly along river valleys. (D.A. Westworth and Associates 1979).

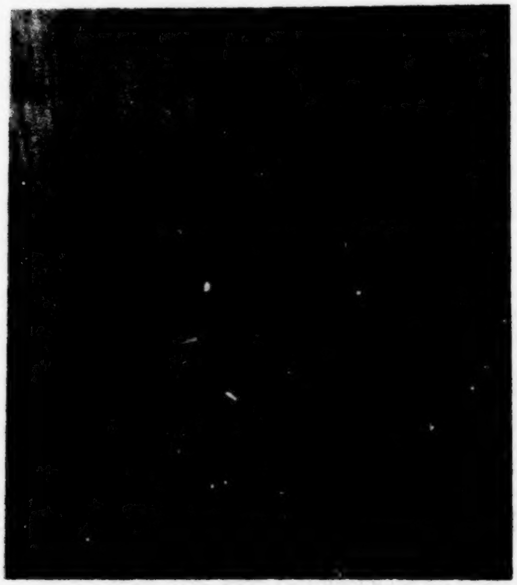


Figure 38. ALLUVIAL AREA OF WILLOW USED BY MOOSE FOR WINTERING (Courtesy of L.M. Allison, Salix Enterprises Ltd., Cowley, Alberta)

In the Northwest Territories, rivers are major travel routes for native people in winter and summer. Moose are shot whenever they are encountered, and have apparently been eliminated from excellent island wintering habitat near communities (Walton-Rankin 1977). Moose populations in other alluvial areas of the Mackenzie system, for example the Liard River valley, are heavily harvested and numbers taken may currently be at or near sustainable yield (Donaldson and Fleck 1980).

Mule deer occur in southern parts of the Mackenzie River Basin, but are scarce in the Northwest Territories. Their populations are limited by snow depth and severe winters. Along the upper Peace River, Blood (1979) recorded their greatest use of river floodplains and islands to be in summer during the fawning and post-fawning periods. Winter ranges of deer in the area were almost entirely on valley slopes above alluvial sites (Blood 1979). Near Fort McMurray, mule deer occupy aspen and mixedwood forest types, showing a preference for variable topography and edges or ecotones. Wintering areas are largely along major river valleys (D.A. Westworth and Associates 1979). In both areas the habitats chosen for wintering by mule deer are the same - aspen and mixed woods along a major river valley. In one area, such habitats are found on alluvial sites; in the other they are not.

The importance of river valleys to populations of ungulates, especially in winter, is underscored by the habitat patterns shown on maps of the Canada Land Inventory which illustrate land capability for ungulates. Bands of important habitat for ungulates, particularly wintering habitat, often follow rivers, although much of the important habitat is above the floodplain. Populations of ungulates that spend the summer on intervening uplands depend for their maintenance on the continued availability of wintering habitat in river valleys. For example, elk prefer forested habitats interspersed with open grasslands, generally in non-alluvial areas. However, they also successfully inhabit mixedwood forests in central Alberta, concentrating in winter along river valleys where the snow is not too deep (D.A. Westworth and Associates 1979).

Historic ranges of the wood bison included the Mackenzie River Basin in the Northwest Territories as far north as Fort Simpson plus parts of Yukon and Alaska (Reynolds 1979). The native wood bison bred freely with plains bison introduced from Alberta, producing a hybrid. Bison are currently found in Wood Buffalo National Park, in the Mackenzie Bison Sanctuary which is a non-alluvial area of glaciofluvial origin, and on the Slave River Lowlands near Hook Lake. The Slave River Lowlands support large areas of sedge and grass meadows which provide excellent habitat for the hybrid population of bison. During summer, activity of bison centres on large open meadows. In winter they feed on smaller meadows but rest in sheltered forested areas (Reynolds et al. 1978), like bison on the Peace-Athabasca Delta (Allison 1973b). During all seasons, slough sedge and reedgrass are the preferred food species for bison (Reynolds et al. 1978).

Blood (1981, pers. comm.) commented that the importance of river valleys to ungulates in the southern part of the basin is more a result of physiographic and climatic diversity than current alluvial processes. In southern parts of the basin, valley slopes which may be a result of former alluvial processes are more important for wintering of ungulates than the active floodplain (Figure 39).

Many of the alluvial areas discussed in the report, and much of the wildlife habitat, is not within the active floodplain and under most current conditions is not subjected to fluvial processes. River terraces, for example, are protected from most floods and support plant communities of later seral stages than does the active floodplain.

The type and origin of parent material is only one of the factors that collectively determine which plant communities will be found on river terraces and valley slopes and which locations will be attractive to wildlife species. Slope, aspect, physiography, microclimate, structure of the plant community, and species of plants and animals present are all important.

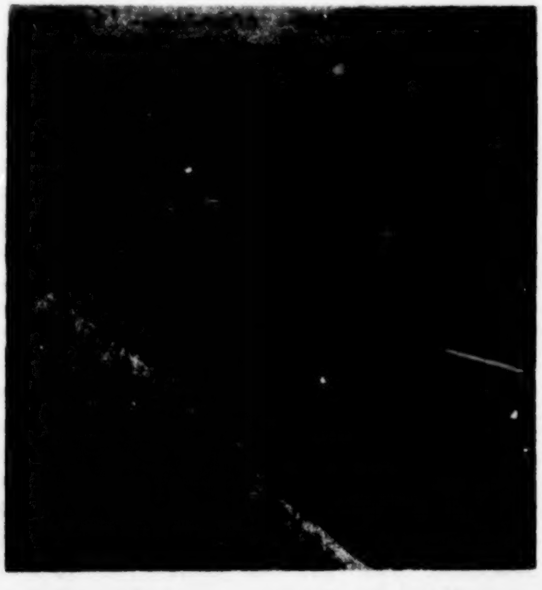


Figure 39. UPPER REACHES OF THE ATHABASCA RIVER VALLEY PROVIDE WINTERING HABITAT FOR A VARIETY OF UNGULATE SPECIES (Courtesy of Dr. Don Gill Memorial Slide Collection, University of Alberta, Edmonton)

C. Comparisons of Wildlife Species and Habitats on Alluvial and Non-Alluvial Areas

All major wildlife species of economic importance in the Mackenzie River Basin which find suitable habitat in alluvial areas are also found in some locations of non-alluvial origin. Regardless of whether an area is alluvial or non-alluvial in origin, if it provides the necessary type and structure of plant communities and the other physical habitat requirements for a wildlife species, that species will usually inhabit the area. However, most upland areas in the Mackenzie River Basin support quite a different assemblage of plant and animal species than do alluvial areas. Direct comparisons of population densities and other population parameters between such areas are not possible because data are unavailable.

Data are not now available to compare the annual rate of production of herbivorous animals (secondary productivity) on alluvial and upland locations. The impression of high productivity in animal biomass on alluvial areas may or may not be confirmed when such data have been collected.

A few locations such as the glaciofluvial Brackett Lake wetlands seem similar in physical and vegetational features to alluvial wetlands and support some of the same wildlife species. The Brackett Lake wetlands have been repeatedly disturbed by fire and support a variety of successional plant communities. Parts of Brackett Lake and Loche River remain open all winter and provide attractive early resting sites for migrating waterfowl in spring. The wetlands are an important fall staging area for arctic nesting waterfowl in all years and may be of critical importance when poor weather conditions prohibit staging along the coast (Dickinson 1978). Most of the area is also excellent or very good waterfowl production habitat (Poston et al. 1973). The Brackett Lake wetlands provide the best muskrat habitat in the Northwest Territories. Although the status of beaver in the area is not known, the wetlands are excellent habitat and are capable of supporting stable populations of beaver (Dennington et al. 1973). Although the Brackett Lake wetlands are only fair winter range for moose, they are important because moose winter habitat is scarce in a relatively large surrounding region (Prescott et al. 1973).

The example above illustrates the fact that concentrations of wildlife that are associated with alluvial ecosystems may also be found in non-alluvial locations where their habitat requirements are met. Such habitats may be the result of repeated disturbance by fire. However, non-alluvial areas that support concentrations of the same wildlife species as in nearby alluvial areas are relatively uncommon in the basin. The distribution of channel systems throughout the basin forms a constantly shifting assemblage of alluvial sites which are used by a variety of wildlife. The erosive and building actions of fluvial processes along waterways maintain a virtually permanent diversity of habitats and the drainage pattern determines that alluvial habitats are distributed throughout the basin. From alluvial locations, wildlife populations may expand into upland habitats which become suitable, often as a result of fire, with the result that wildlife populations that find important life cycle requirements fulfilled by alluvial habitats can be well distributed throughout the basin.

D. Nutrients Available to Wildlife in Alluvial Ecosystems

It is commonly stated that alluvial sites are more productive for vegetation or wildlife than other types of parent materials (Gill 1973b). As outlined in Chapter V, a relatively high primary productivity of certain floodplain sites can be substantiated, but whether this is also translated into a correspondingly high secondary productivity is not so readily apparent from the available ecological knowledge of flood-prone areas.

Flooding with silt-laden waters offers an annual replenishment of mineral nutrients and organic matter. By implication, floodplains and delta lakes which are not connected to rivers will become increasingly nutrient deficient unless silty floodwaters flow in over levee banks (Gill 1973b). Flooding, by periodically destroying plant communities, also ensures that alluvial habitats generally remain in relatively early successional stages. Biomass accumulation on young successional stages tends to be more rapid than in climax vegetation and, where this is the case, more of the energy fixed may be available to wildlife than in mature ecosystems. Without continued initiation of primary plant succession, the productivity of any northern delta or floodplain for wildlife would diminish (Gill 1973b).

Data which directly compare nutrient values of plant species used by wildlife on alluvial areas with nutrient values of plants used by wildlife on non-alluvial areas are generally unavailable. Some discussion of nutrient values of food plants chosen by wildlife species is possible, although the available data do not generally distinguish alluvial and non-alluvial sites.

Muskrats eat a variety of early succession emergent plant species, with cat-tail being considered their most important food source. Muskrats on the Peace-Athabasca Delta, on a lake with no cat-tail, showed clear preferences for sweetflag, bur-reed, and sedge. Use of the submerged plants, milfoil and pondweed, were not estimated although it was recognized that they are commonly eaten in winter. There was a positive correlation between preference and nutrient ranking, although it was not tested statistically (Westworth 1974). In the absence of comparative data on muskrats elsewhere, Westworth (1974) noted that the nutrient content of plants eaten by muskrats on the Peace-Athabasca Delta falls within the range acceptable to domestic herbivores. At best, these data can be used to establish a base level adequate to support a muskrat population.

Browse selection by moose in the Fort Providence area could not be statistically related to browse nutrient content. Although moose showed a marked preference for certain species of willow and an avoidance of others, they seemed to be selecting species of lower nutrient content (Penner 1978). Reasons for preferential use of certain species may involve nutrient content, but may also include succulence, shrub height, growth form, season of use or type and abundance of associated plants (Berg and Philips 1974).

Winter browse available to moose near Fort Providence was approximately 20% of summer browse production. Previous browsing increased the probability of re-browsing. After simulated or natural browsing during the dormant period, willow responded with a decrease in the number of twigs and a two to four times increase in twig weight in the following season. The larger twigs may have influenced preference of moose for such shrubs (Penner 1978).

Nutrient requirements for moose have not been established. However, if their requirements are similar to those of white-tailed deer, the willow browse around Fort Providence was adequate for growth during spring and early summer, but in winter would only be marginally adequate for maintenance. Moose in winter may conserve energy through foraging efficiency, by maximizing intake while minimizing movement (Penner 1978). Although the suggestion has not been scientifically tested, alluvial habitats may be the most energy-efficient sites for moose wintering, by providing a concentration of acceptable food of a single species, such as a certain willow, near conifer stands where shelter can be found.

Pavlov (1976), in a Russian work, suggested that the state of water in some plants in winter may be important to moose, and may influence food preferences. Water in some species remains in a liquid state at below freezing temperatures. During severe winter weather, moose favour forages that retain water in fluid form. For instance, floodplain willow remain soft and flexible in winter and are consumed more readily than are the more brittle aspen and pine (Pavlov 1976).

In parts of Alaska, up to 94% of the winter diet of willow ptarmigan consists of buds and twigs of willow, and up to 80% may be one species, Alaska willow. In fall, several willow species, and where available, birch and aspen are used. However, as snow depth increases to cover lower growing species, taller plants such as Alaska willow are used more and more heavily. Birch, aspen, and alder buds have a higher caloric content than willow at all seasons because of their higher lipid content. However, alder is seldom used by willow ptarmigan even where abundant, suggesting that they are unpalatable. The nutritional value of willow buds remains relatively constant during fall and winter, then rises in May prior to flowering. Nutritional values fall to a seasonal low in June, before rising to the fall and winter levels (West and Meng 1966).

Summer diets of adult willow ptarmigan in Alaska contain willow leaves, herbaceous plants and berries in addition to willow buds. Willow catkins and leaf buds are dominant food items in June, young willow leaves and maturing willow seed capsules in July, willow leaves and buds and the seeds of grasses in August, while berries are believed to be important in September (Williams et al. 1980). In June, catkins have relatively high caloric values and concentrations of nitrogen and phosphorus peak at that time. In willow leaves, concentrations of nitrogen and phosphorus are highest in July. The caloric content of willow leaves in July is similar to that of buds during winter months. By September, willow leaves lose much of their nitrogen and phosphorus and are poorer nutrient sources than berries (West and Meng 1966).

Young willow ptarmigan utilize insects and herbaceous plant parts in early life, with increasing amounts of willow leaves as they mature during the summer. Willow ptarmigan display a strong preference for leaves of deciduous shrubs in all habitat types along the Meade River, Alaska. Except for Dryas, willow ptarmigan avoid the leaves of evergreen shrubs, although all types of berries are utilized. Rodents in the same area also avoid the leaves of most evergreen shrubs (Williams et al. 1980).

Levels of nutrients in plants are only one factor that may influence food choices of animals. Other parameters that may be selected include availability, growth form, succulence, palatability, type and abundance of associated plants, and nearness to other habitat requirements. Although baseline information on nutrient availability in some alluvial areas in the basin and Alaska is available, it is sparse and inconclusive. Data are insufficient to allow any conclusions about nutrients in alluvial areas to be reached. Comparisons between alluvial and non-alluvial areas, in terms of nutrient content of plant species, are not possible.

CHAPTER VII

ECOLOGICAL PROCESSES IN ALLUVIAL ECOSYSTEMS: A SYNTHESIS

The following chapter highlights ecological processes that are specific to or occur in alluvial ecosystems. The term, ecological processes, is interpreted broadly to include the concept of ecological niche. The latter term is variously used in the ecological literature to refer to the physical space occupied by an organism, its functional role in the community, or its position in environmental gradients (Odum 1971). To avoid confusion that could arise from the diverse meanings of ecological niche, the term is not used. Instead, the focus is on links between fluvial and biological processes, relationships among organisms in alluvial ecosystems, and relationships between organisms and physical processes. The chapter is a synthesis and interpretation of material presented and referenced in earlier chapters. To avoid interference with the discussion, most references previously cited are omitted from this synthesis.

Ecological processes and relationships summarized here are controlled by water. Water is a prime shaper of the landscape - both a destroyer and a builder. Wherever the flow of water is strong enough to carry away soil particles, it erodes. Further downstream, sediments are deposited and new landforms are built in low-lying areas along stream channels and in deltas. These alluvial landforms are sites with complex and ever-changing relationships among fluvial, geomorphic, and biological processes.

The dynamic nature of alluvial sites is emphasized by all who have studied such habitats. Each site is subject to change, first by aggrading processes as sediment is deposited, then by a combination of physical and biological influences through the development of a series of plant communities and associated species of animals, and then eventually by destructive physical forces that either erode alluvial sites or cover them with new layers of sediment. Although the factor of change is central to productivity of alluvial sites, there is also a relative overall stability within alluvial ecosystems.

The apparent contradiction between continuous change and relative stability can be understood if one makes a distinction between alluvial sites and alluvial ecosystems. Alluvial site refers to a point location at which a process of aggrading or degrading is occurring at any given time. Alluvial ecosystems refer to a complex of alluvial sites, the components of which each change with time, but which in combination provide a relative stability in any given flood-prone area by providing a more or less constant set of habitats for plants and animals. Although features found at a specific site differ over a period of years, the general nature of deltas and river valleys remains in a state of disclimax dynamic equilibrium.

Physical and biological processes in alluvial sites of the Mackenzie River Basin are strongly influenced by the fact that spring break-up and the snowmelt flood are the major hydrological events each year in rivers and deltas of the basin. The presence of large volumes of river ice encourages ice jams at river bends and in areas of shallow shoals and such dams produce flooding that may both precede and exceed runoff associated with the snowmelt flood. Occasional summer rainstorm floods in the Mackenzie River Basin produce flood waters higher than floodwaters in spring, especially on rivers with mountainous headwaters. In general, rivers of the basin are characterized by low water levels that are broken only by high water levels during break-up floods, during the period of snowmelt, during intermittent and unpredictable summer storm floods, and sometimes during freeze-up when accumulations of frazil ice cause flooding.

Although flooding is emphasized in hydrological accounts of water levels, flooding height is not the only feature of importance to plant and animal communities. Outflow, percolation, or evaporation of floodwater, collectively referred to as recession, is also thought to be ecologically important, although it is not well documented. It is known that timing of recession during the summer growing season is one factor that determines which plant species can establish themselves in exposed areas. Changes in flow regime that do not influence maximum flood levels but do influence duration of floods and rate of recession can have major effects upon plant and animal communities, as indicated by ecological events on the Peace-Athabasca Delta.

A. Fluvial Processes that Build Alluvial Habitats

Building phases of alluvial activities generally attract less attention than erosional features that result from movement of water over land. One of the reasons for the relative lack of attention to depositional phases of the geomorphic cycle is that erosional features tend to be the areas of greater visual contrast and sharper topographic relief whereas water-borne sediments are laid down as low relief alluvial deposits. It is easy to overlook the fact that within a drainage basin every place of water erosion is matched by a place of sediment deposition. While high water levels, ice jams, and ice-shove ridges are among the more dramatic physical aspects associated with spring break-up, the less dramatic but continuous erosion and rebuilding of alluvial landforms in river channels and in deltas are the dominant forces involved in the complex web of ecological relationships in flood-prone areas.

Changes in land surface and drainage occur so rapidly in alluvial sites that it is difficult to think of alluvial sites except in terms of successional development. The major factor causing ecological change is the increasing elevation of surfaces over time due to deposition of alluvium. This deposition has three important effects: the internal drainage of soils increases with height above the river; the period of time that sites are under water during flooding is reduced with increasing height above the river; and the yearly amount of sediments added to the surface decreases with height above the river.

The building of alluvial habitats takes place mainly by deposition of sediment from floodwater, although water-transported organic debris and direct accumulation of plant and animal material within alluvial ecosystems also add to the aggradation process. Island building, point bar formation, levee building, and general deposition of sediment over the surfaces of floodplains and terraces are the prime building steps associated with floodwaters. Other specialized landforms may be formed in alluvial areas, including ice-shove ridges along portions of stream channels subjected to repeated ice jams, small reverse deltas built into delta or floodplain lakes that are joined to a river by a connecting channel, or wind-deposited layers of mineral soil that may be shifted from channel edges during dry periods of low water. However, such landforms are generally localized in distribution and are secondary to the overwhelming dominance of sedimentation as a building process in alluvial sites.

The physical mechanisms by which terraces, floodplains, levees, islands or point bars are built are too complex to summarize here. However, a brief account of the point bar environment, which has been documented in considerable detail within the Mackenzie Basin is illustrative of the biophysical links between fluvial building processes and subsequent biological events on depositional landforms. Helicoidal flow has been identified as the prime physical force behind formation of point bars in the Mackenzie Delta. Such flow occurs along shifting sections of a channel and it is a result of the fact that in a channel the maximum rate of flow is attained by water that flows near the concave bank, the outside curve where bank erosion occurs. Surface water there plunges downward and is directed along the bed of the channel toward the convex bank; this cross-channel flow is called helicoidal flow and it results in coarse bed materials being swept laterally to the convex or inside bank of the channel where they are deposited. Such cross-channel movement of sediments is the principle mechanism in construction of point bars. As sediment build-up enlarges point bars, their crests eventually surpass normal flood levels and once the physical constraints of flooding and high sedimentation rates have been reduced, a distinct plant community of balsam poplar dominates virtually every point bar in the Mackenzie Delta. Point bars in the delta are built mainly during the annual mid-May to mid-June flood period, and their heights therefore are usually coincident with average flood stage which tends to be about 3.5 m above mean summer channel level.

An integral part of point bar formation is the concurrent creation of successive meander scroll depressions. As a point bar extends itself into a meander curve, a series of alternating arc-shaped ridges and depressions marks the successive, individual depositions. The depressions, located inland from each successive point bar, impound local runoff until they eventually fill with fine sediments deposited during flood stage. The attraction of meander scroll water impoundments for beaver and the nearby point bars with a natural cover of balsam poplar, an important food source for beaver, are an example of the links that may exist between processes of fluid dynamics, sedimentation, sediment sorting, vegetational development and wildlife occupation of alluvial ecosystems.

The volumetric role that organic matter may play in the build-up of delta surfaces has not been studied in detail. It can be expected that the relative importance of organic matter as a component of deposition would be greater in regions of continuous permafrost than in warmer climates because decomposition is arrested when perennially frozen ground prevails. In the Mackenzie Delta, flood stage brings organic debris that ranges from large logs to microscopic particles and there have been estimates that organic matter makes up as much as 25% of the total volume of silt exposed in channel banks of the delta. Such estimates indicate the potential importance of nutrient re-deposition during floods. As outlined in a later section of this chapter, plant succession is usually initiated on new alluvium that has been deposited during floods.

Deltas can be ecologically subdivided on the basis of differences in degree or intensity of depositional processes; active, semi-active and inactive areas of deltas have been distinguished. The active delta, involving channels, point bars, levees, and plains surrounding open basin lakes, is directly affected by flooding. The semi-active delta, involving perched basins and cut-off stream channels, is not directly connected with the main hydrologic system, but is recharged by overland flow of water during flooding. The inactive delta, made up of closed basins, old meander scrolls, and other swampy areas, is higher in elevation and is influenced by flooding only at extremely high water levels. Because inflow of nutrients to deltas depends heavily on silt in floodwaters, the sequence from active to semi-active to inactive forms a series that is increasingly deficient in nutrients.

B. Fluvial Processes that Destroy Alluvial Habitats

The predictable successional sequences on alluvial sites are sometimes interrupted by other events. For example, within the Mackenzie River Basin, catastrophic floods, with an estimated return frequency of 150 years, occurred along the Hume River during the summers of 1970 and 1971. Mature balsam poplar and white spruce trees were toppled but not carried away. Alder, willow and balsam poplar suckers began to revegetate disturbed areas very quickly, but the original sequence of primary succession had to be re-established on the new surfaces left by the floods from summer storms.

Some features of specific alluvial sites are developed and maintained by erosive forces. For example, when ice flow during break-up is hampered by a channel bend, rafts of ice may be pushed along the bank several meters above maximum flood levels. Pressure exerted by the moving ice scours away vegetation and soil. The result is a ridged zone of poorly developed vegetation that remains in a state of early successional development along the slopes of river channels where ice rafts are lodged each spring. A secondary effect in some places is a loosening of soil by ice scour so that rainstorms and high water levels in summer can easily wash away the loose soil particles. Ice scour zones occur throughout the Mackenzie River Basin on a variety of alluvial landforms. In some areas ice scour produces boulder or gravel pavements along the river. Here scattered willow and a few herbaceous plants are the only vegetation. However, even such barren-looking areas provide habitat for some wildlife. A few species of birds such as Canada geese, spotted sandpiper and nighthawks nest in ice-scour zones.

Thermokarst lakes are a special erosive feature of older parts of the Mackenzie Delta. Levees surrounding such lakes are underlain by permafrost although the lakes themselves have a mean annual temperature above freezing. The levees are therefore continually eroding into the lakes as ice in silts and clays is thawed by heat transmitted from the water. Establishment of aquatic vegetation on the margins of thermokarst lakes is impossible.

Ice action on some delta channels exerts a mechanical control over some plant communities. It shears off the tops of shrubs as well as above and below ground parts of rhizomatous plants. It may also remove large amounts of sediment from levee slopes, preparing the way for fluvial erosion of the partially bared slope once the soil melts. Water erosion may undercut the channel bank, leaving an unstable ledge that cannot support its vegetation and eventually falls into the channel.

Some parts of the Beaufort Sea coast, including outer parts of the Mackenzie Delta, are subject to rapid erosion, but other parts are advancing.

Summer storm surges accelerate erosion. Shoreline retreat during a major surge may be as much as 20 m and the eroded material is moved and re-deposited by longshore currents.

Erosion caused by floods that result from intense rainstorms in summer may exceed the erosive effects of the snowmelt flood, in part because storm floods consist of warmer water acting on at least partially thawed soils. Floods from summer storms have been known to remove small channel islands and whole stands of trees.

Interruption of vegetational succession by channel bank erosion and the regular replacement of older soil-vegetation complexes with new surfaces that contain nutrients in both mineral and organic forms is a feature that is thought to contribute significantly to the relatively high primary productivity of alluvial sites. Although quantitative data are generally lacking, it is suspected that periodic redistribution of nutrients from one place to another within flood-prone areas is a process of fundamental importance in the successional sequences and productivity levels of alluvial sites.

If older portions of a floodplain are not periodically destroyed by lateral erosion, vegetational succession generally leads to a closed-canopy coniferous forest in which there is a progressive build-up of nutrients in ever-deepening humus layers; the mature forest community becomes increasingly isolated from the nutrient supply that comes from annual flooding and siltation. Ecological links such as those outlined above emphasize the importance of floodwaters as a physical force that creates the disturbances necessary for nutrient renewal in alluvial ecosystems.

C. Annual Fluvial Processes that Influence Alluvial Vegetation and Wildlife

By definition, floods involve fluctuations in water levels. Apart from their effects on the building and destruction of alluvial landforms, annual fluvial processes such as flooding, recession of water levels, and ice jams may have direct influences upon plant communities and resident wildlife.

High water during spring break-up lifts, breaks and removes ice from the Mackenzie Delta. Nearly half of the delta is covered by lakes and channels, so the change in albedo caused by flushing of ice during spring break-up can be significant. In addition to removing ice, floodwaters also inundate all but the highest levees on the delta so that high-albedo snow surfaces are flooded and a relatively high amount of short-wave radiation is absorbed as soon as floodwaters subside. On areas adjacent to the delta where there is not the benefit of ice removal by flooding, lakes remain ice-covered for up to one month longer than nearby delta lakes. The relatively rapid warming of the delta allows establishment and growth of white spruce and balsam poplar and creates one of the most northerly extensions of the boreal forest in North America.

The wide variety of relationships between vegetation and hydrologic events is exemplified by the many scientific uses of plants as indicators of floods, sediment deposition, and channel migration. Dendrological methods used to determine dates and magnitudes of floods and sedimentation on modern floodplains include analyses of: annual ring growth around tree trunk scars; growth of sprouts from water-felled trees; growth of trees after burial by alluvial sediment; and relationships between floodplain trees and low flow. Driftwood on river banks is a commonly used indicator of maximum flood level. Driftwood stranded at high elevations above the river channel generally results from ponding of water behind ice dams but sometimes it is a result of high water levels during summer storms. Injuries to the bark of trees growing on river banks in the Mackenzie River Basin are indicators of maximum ice-shove levels. Willow ages have been used to estimate minimum periods of channel bar stability and adventitious roots of spruce have been used to document rates of sediment addition to floodplains.

Waterfowl use deltas of the Mackenzie River Basin for both staging and nesting, although the habitat requirements for staging are different than they are during the nesting period. Conditions for staging seem best when water levels are relatively low, although the mudflats and early pioneer vegetation types that attract ducks, geese, and swans can only be maintained by periodic flooding and subsequent reductions in water levels. Broad areas of open mudflats and peninsulas provide security from terrestrial predators and early succession vegetation provides food. Virtually all of the northern- breeding migrants that use the Central and Mississippi flyways use at least one of the deltas of the Mackenzie River Basin for staging in spring or fall. Numbers of staging birds using northern delta areas are lowest under extreme flooding, when high water extends beyond normal shorelines into willow or forested areas.

For optimum production of waterfowl, nesting habitat must be maintained throughout the nesting season. Although a relatively small decline in water level would not significantly reduce nesting success, increases in water level can cause severe losses as nests are flooded. Restricted drainages that are re-charged by some floods, but are not directly connected with open basins, seem to support the highest densities of nesting ducks in deltas. Periodic flooding is necessary to maintain the variety of habitats attractive to nesting birds even though highest production may occur after several years of low water levels.

River valleys may be used by waterfowl during spring because open water becomes available earlier along certain parts of the channel than it does in nearby lakes. Leads along shorelines and around islands open early and pools of water often appear where tributaries meet a main river channel, before the ice moves out of the main channel. Numbers of birds using such areas are relatively low in comparison with deltas. Nevertheless, break-up along the Mackenzie River and its tributaries does provide significant spring staging habitat. The fact that pairing and mating of some waterfowl species may take place along river channels during the spring flight is particularly important. For example, islands of the Mackenzie River near Norman Wells are locations where lesser snow geese pair and mate.

Complex interactions of water levels and vegetation combine to maintain appropriate habitat for muskrat populations, but there is some cost in certain years to individuals in the population. Muskrats live around the margins of delta lakes either in bank dens on steep banks or in lodges built of emergent vegetation. Lodges are not used regularly north of 60° N. Emergent vegetation such as cat-tail, bulrush, and other species are used for food as well as for house construction. In winter, particularly, submerged plant species such as milfoil and pondweed are also used.

Water level requirements for muskrats and the difficulties of survival for individuals are related to physical requirements of plant species that muskrats depend on and also to the problem of survival in winter. Although it is possible for muskrats to survive in parts of lakes that freeze to the bottom, their opportunities for overwintering successfully are increased if the lodge or den is located in an area where free water remains under the ice. Why, then, do muskrats not simply move into deeper water for winter? Neither emergent nor submerged plant species can become established or survive in deep water. Food and housing requirements of muskrats restrict them to shorelines and relatively shallow lakes where there is a danger of freezing out in some years. Pushups are mounds of submerged vegetation that are pushed up onto the surface of forming ice in fall. They become covered with snow and form insulated feeding ledges which are maintained by the muskrats all winter.

Requirements for the establishment and maintenance of emergent stands of vegetation also complicate the situation. To the muskrat, a healthy stand of emergents is most attractive when it is standing in the deepest water possible. However, continued viability of such stands requires periodic lowering of water levels. Seeds of some species will germinate successfully only on exposed mudflats. Relationships between muskrats and flooding depend upon the fact that maximum natality and minimum natural mortality in the muskrat population occur when water levels are relatively stable at a relatively high level and good habitat is available. However, regular flooding and recession of water levels are required to maintain good habitat. Flooding results in deaths from drowning, and low water levels result in increased winter mortality. Delta wetlands provide the variable conditions necessary for optimum muskrat habitat.

The Peace-Athabasca Delta is the only one of the three deltas that supports bison. Although hybrid wood-plains bison are found in other areas, both within and outside of Wood Buffalo National Park, greatest concentrations and largest herds can be found on the delta under most conditions. As with some other delta wildlife, notably waterfowl, bison populations thrive in years of relatively stable and low water levels, but they depend on changing water levels to maintain their habitat. In all seasons, bison on the delta eat primarily sedges and some grasses. Horsetail may also be eaten in spring. In spring and summer, bison concentrate on the broad sedge meadows, but in winter they move into sheltered clearings where the same food species are available.

Ironically, like other delta wildlife, bison are subject to injury and death from the same physical features of the environment that they depend upon for a continued supply of suitable habitat. Drowning can be a major cause of bison mortality during high floods, yet it is the changing water levels that create their needed habitat. In some years estimates of deaths from drownings have been as high as 3 000 in the Peace-Athabasca Delta area.

The Peace-Athabasca and Slave deltas are freshwater; in the basin only the Mackenzie Delta is estuarine. White whales are the only marine mammal to occur in large numbers within the zone of influence of the Mackenzie River. They move into turbid estuarine areas in late June, apparently attracted by the warm water which they are thought to require for calving. Whales that frequent the Mackenzie River estuary are the only population of white whales in the western Canadian arctic region. Although the function of the Mackenzie River estuary in the history of the population is not understood, the area is believed to be critical to survival of these whales and the warmth of the Mackenzie River water - up to 15° C - is considered a major factor.

Complexity of delta ecosystems and the importance of a variable hydrological regime to ecosystem maintenance is underscored by the situation on the Peace-Athabasca Delta since 1968. Closure of the W.A.C. Bennett Dam on the Peace River caused abnormally low water levels for several years. Vegetation succession proceeded rapidly and it was clear that wildlife populations on the delta would suffer. Remedial measures, in the form of weirs, were installed. Use of the weirs did not enable the imposition of a natural hydrologic regime on the delta and it seems clear that under the present circumstances populations of muskrat, bison, and waterfowl cannot be maintained at pre-dam levels, nor are their habitats comparable to conditions before dam construction.

Experience on the Peace-Athabasca Delta has made it clear that relationships between certain plant communities and flooding may be extremely complicated. Apart from height of flood levels, factors such as timing of the flood, its duration, and speed and level of water recession are all important. As an example, the physical changes that accompany low water levels in winter can be of particular biological significance for some species. Channels and streams freeze in fall, prior to reaching their lowest levels for the year. When water levels drop, the ice will drop to rest on the water. However, at the shore an ice ledge remains above a protected air space. Muskrats may use the air space to feed on horsetail exposed by the receding water. However, when using the sub-ice air space muskrat are vulnerable to predation from mink which also forage under the ice.

D. Vegetational Influences upon Physical Processes in Alluvial Habitats

It is common to think of relationships between physical and ecological processes as though they consisted entirely of effects of the physical environment upon biological components. However, the vegetation on alluvial sites significantly influences the effect of some physical processes. Sediment and vegetation are strongly interrelated within the total floodplain system. For example, along the Beatton River in British Columbia, deposition of sediment averaged 6.1 cm/yr and totalled 2.5 m over a fifty year period in young balsam poplar stands. Underneath mature balsam poplar and young spruce, deposition averaged only 0.8 cm/yr; mature spruce stands were flooded but deposition of sediment was negligible. The rate of deposition is greatest where the closeness of stems causes floodwater flow rates to decrease. In the Mackenzie Delta, willow zones averaged 8 cm/yr of sediment deposition, and in one flood 0.42 m of sediment was deposited in a dense stand of willows. High rates of sedimentation on the youngest surfaces are probably due to the combined effects of their proximity to river channels and the high densities of stems found there.

An indirect link between climate and the effects of floodwaters involves equilibrium levels of the active layer. Development of perennially frozen ground is encouraged by build-up of organic material. On actively silting floodplains, regular deposition of sediment during floods discourages the growth of mosses and other ground cover that would provide insulation to aid ground ice formation. In the absence of flooding and regular siltation, organic matter accumulation is no longer retarded, leading to increased moisture content of soils, reduced soil temperatures, and reduced active layer depths. Such processes have direct influences upon the development of vegetation on flood-prone areas.

Although flooding sometimes occurs on alluvial sites dominated by white spruce, sedimentation is negligible because the spruce zone is normally a considerable distance and elevation from the source of sediment. With increasing dominance of white spruce in the canopy there is an increase in the amount of moss cover on the forest floor, often forming a continuous and luxuriant carpet. A spruce canopy reduces the amount of sunlight reaching the forest floor and, combined with the insulative effects of mosses and organic material, cooler and wetter soil conditions result. In areas of continuous permafrost the cooler, wetter soil conditions result in a decrease in depth of active layer, compared to previous successional stages. Where permafrost is not continuous, frozen ground or permafrost may become established under white spruce stands. Vegetation-active layer relationships in alluvial sites differ from those on upland sites mainly by the more restricted occurrence of perennially frozen soil in alluvial areas. For example, along the Beatton River floodplain in northeastern British Columbia, frozen ground was present only under mature white spruce stands. Similarly, along the Chena River floodplain in Alaska, permafrost most readily formed under older white spruce stands.

On point bars of the Mackenzie Delta, perennially frozen soils are present beneath all vegetation types. However, due to the coarse texture of point bar sediments and the heat energy received through the deciduous canopy of balsam poplar, areas underneath poplar stands have a warmer and deeper active layer than most other sites in the Mackenzie Delta. This soil warming occurs earlier in the spring underneath poplar stands than it does under other vegetation types and allows poplar to break winter dormancy earlier than other species.

On rapidly prograding levees along shifting channels in the Mackenzie Delta, some areas of permafrost-free soil are characterized by a willow-horsetail vegetation type. Such areas of unfrozen ground are estimated to cover 8% of the Mackenzie Delta and are thought to be a result of thermal influences of the adjacent channel in which the mean annual temperature may remain above freezing. Insulation created by snow drifts within and on the edges of willow stands can also help to maintain soils free of permafrost.

Vegetation along stream channels can have an influence upon the reaction time associated with variations in discharges of water and sediment. In the absence of major floods, vegetation continually encroaches on the stream channel, reducing the rate of change of bank position. Effects such as these would be negligible in large rivers such as those that drain the main sub-basins of the Mackenzie River Basin. In small tributaries, however, the effects of vegetation are evident, with the result that well-vegetated channels tend to be narrower than those without vegetation. If a channel loses its fringe of vegetation cover, the unprotected channel will tend to become wider than the original. When trees are removed by major floods they may further interact with geomorphic processes downstream where floating trees become part of the debris responsible for jams, flooding, and channel diversions.

Unvegetated faces of point bars in the Mackenzie Delta are subject to wind erosion after the deposits are dry enough to be moved by high winds. During winter, wind prevents snow from accumulating on many point bars. Such snow-free surfaces are subject to erosion by wind and abrasion by wind-driven snow. Most of the sand removed from the point bar is deposited just within the leading edge of vegetation where wind speed is reduced. As the point bar builds outward, willow and poplar move outward and are followed by other successive bands of vegetation. A deep snow drift forms at the same general location every year, just behind and parallel to the leading edge of vegetation.

E. Long-term Successional Processes in Alluvial Habitats

Plant communities on alluvial habitats change in predictable ways with time. Although succession may be interrupted by some of the processes described earlier, long-term trends can be outlined.

Plant community types found in deltas include aquatic communities in open water, shore communities, emergents that grow on mudflats, meadow communities, shrub communities, and forest communities. Plant succession on various delta sites does not follow a single pathway but takes the form of a branching network in which several distinctly different species or species groups may dominate apparently identical sites during some specific successional stage, and then give way to a single plant community at some succeeding stage. It is not clear why sites that appear to be physically and successionally identical are occupied by different species groups; the supply of plant seeds at the time when conditions happen to be favourable for germination is probably an important factor. In general, however, most delta areas have a vegetational sequence that begins with aquatic and emergent communities which are replaced by shoreline pioneers on exposed mudflats and then eventually by meadows. Meadows are, in turn, replaced by willow-shrub communities, which give way later to poplar and finally coniferous trees. The most mature communities are found on the highest and best defined levees.

Extensive, very flat sedge and grass meadows on the Peace-Athabasca and Mackenzie deltas are periodically flooded by standing or slowly moving water. The water table extends as high as the rooting zone for part of the growing season. Meadows, levees, and perched basins all receive some sediment when flooding occurs. However, the rate of deposition is relatively slow in locations distant from sources of sediment. In inactive delta areas, lack of regular flooding results in gradual fixing of available nutrients in undecomposed organic material. Floating sedge mats grow over entire ponds which eventually fill in with mud and peat, developing into bogs.

In active delta areas under natural conditions, succession to drier vegetation types may be slow. For example, it took more than 40 years for a sedge-dominated meadow on the Peace-Athabasca Delta to succeed to grasses and some willows. Even then, some of the change noted was probably a result of general drying of the delta after closure of the W.A.C. Bennett Dam.

Under most natural circumstances, succession on a delta is controlled primarily by water regime. If water levels decrease, replacement of one plant community by another proceeds rapidly in early stages but more and more slowly in shrub and forested communities. However, if there is a normally fluctuating hydrological cycle, sites directly influenced by fluctuating water levels tend to be maintained at early successional stages until such processes as channel shifting or levee building drastically alter the local water regime.

Successional zones of distinctively different vegetation types are so prominent on non-deltaic alluvial sites that there are now many textbook documentations of successional trends on floodplains, although there are not many such accounts from within the Mackenzie River Basin. The general successional trends common to alluvial sites within the Mackenzie River basin can be summarized as follows. As soon as the surface is exposed above average summer water levels, colonization by emergent plants, usually horsetail, occurs. When further depositions of sediment raise the surface sufficiently, willow becomes established. The willow and horsetail zones are subject to the heaviest flooding and sediment deposition. When the alluvial surface is raised above the bankfull stage, alder, balsam poplar, and white spruce become established. As balsam poplar mature and die they are replaced by white spruce. Once they become established, willow and alder may remain as understory shrubs throughout subsequent stages.

If continued river meandering, catastrophic floods, or fires do not interrupt the successional sequences, further succession to a black spruce-moss or black spruce-bog type of vegetation is possible. Unlike adjacent upland areas, there is a relative absence of fire as a disturbance on alluvial sites, a circumstance that is thought to be responsible for the great ages of white spruce trees found on some alluvial sites. There are several reasons for the observed lack of fires. Floodplains, river meanders, and oxbow lakes act as barriers to the spread of fires; the frequent presence of seepage sites at the base of steep slopes adjacent to alluvial sites is another deterrent to spread of fires; the large amount of exposed mineral soil after flooding provides little surface fuel for fires; and there is also a relative lack of burnable surface material throughout the floodplain forest floor for a considerable time after each flood period.

The successional sequences outlined here have direct relationships to patterns of wildlife use. Moose depend on early succession plant communities for food, particularly in winter. Alluvial plant communities along river channels and terraces and on minor deltas provide optimum winter habitat for moose. Alluvial areas provide a concentration of suitable food species for moose in association with nearby stands of conifers which are used as cover. Islands may be used by moose in the Mackenzie River Basin as wintering areas and by females with calves in spring.

In the case of beaver, the best sources of food and building material are usually found on older successional stages that support willow, balsam poplar, alder, birch, or aspen. In some locations, a shortage of food appears to limit the period of time a beaver colony can occupy a given location, while at other sites beaver seem to remain indefinitely. A more localized successional sequence, typical of point bars on the Mackenzie Delta, can create a distinct type of beaver habitat. As channels shift, differential flow around curves picks up sediment from the channel bed and deposits coarse alluvium on point bars. Meander scroll depressions which impound local runoff are formed at the same time as point bars. Balsam poplar, a preferred food species for beaver, colonizes the coarse point bar deposits. Beavers are attracted to the site by food, but damming of the nearby meander scroll depression and construction of lodges meets their other habitat requirements.

In some situations, animals can influence vegetational succession as well as being influenced by it. In the case of point bars, selective removal of poplar by beaver alters the flora of point bars to cause secondary succession to occur. If the site is occupied by beaver long enough, alder and willow become dominant. When beaver abandon such point bars, poplar begins to regenerate. After several years the site may again be attractive to beaver.

Another example of wildlife influences upon alluvial vegetation occurs in certain delta lakes that are connected to larger channels by a single small stream which normally drains the lake. Under flood conditions such streams reverse their flow and carry silt-laden floodwater into the lakes. Where the inflowing current meets the water of the lake, silt is deposited in a small delta that projects into the lake - a reverse delta. The newest portions of reverse deltas are covered with grasses. Such sites are the only locations in the Mackenzie Delta that support the grass, **Beckmannia syzigachne.** Seeds of **Beckmannia** are eagerly eaten by ducks, and the plant is thought to be maintained by seeds carried from the south by migrating waterfowl. A second grass species, **Arctophila fulva,** is particularly common on reverse deltas although it also occurs elsewhere. The vigour of **Arctophila** is thought to be encouraged by repeated cropping by waterfowl and nutrient additions from droppings which are high in nitrogen.

F. Adaptations of Plants and Animals for Opportunistic Use of Alluvial Habitats

Areas subject to fluctuating water levels are dominated by plants that have special adaptations to meet such changing conditions. For example, perennial plant species that are able to survive in zones of intermittent flooding, such as willow, alder, balsam poplar, and white spruce, generally have root systems that respond to new deposits of sediment by production of adventitious roots on portions of stems that are buried under sediment. Other adaptations include production of additional rhizomes, as exhibited by horsetail and rushes in flooded areas, or the presence of annual or biennial life cycles that are timed to match the annual drawdown period in alluvial sites such as on the Peace-Athabasca Delta. Adaptations such as these indicate that vegetational occupancy of alluvial sites is not simply an extension of upland vegetation down onto the naturally irrigated flood zones along river channels and on deltas; there is, in many cases, a distinctive set of physiological responses that have evolved to aid survival of plant populations in the variable physical environment that characterizes flood-prone parts of watersheds.

Species of plants that are adapted to take advantage of the special conditions that occur in alluvial habitats are present at all levels in the successional sequence. Water horsetail invades and dominates the newest parts of levees and point bars in the Mackenzie Delta. As well as being able to establish itself in extremely wet soil, horsetail is able each year to grow from rhizomes after above-ground plant parts are buried by alluvium. Once horsetail is established at a site, rapid vegetative propagation allows it to move into newly exposed alluvium.

In general, the plant species that colonize alluvial areas have a variable tolerance to flooding. Among emergents, the common great bulrush will die out in the second year of re-flooding and if the water depth is greater than about 40 cm; cat-tail and some sedges are reduced in abundance and vitality after three years of water depths more than about 30 cm and will die out in the fourth year if such water levels are maintained. Well established willows are the woody plants most tolerant of flooding. They are eliminated only after three or four years of continuous inundation of at least 60 cm.

Although populations of migratory birds, other than waterfowl, have not been studied in detail in the Mackenzie River Basin, it appears that deciduous plant communities support a greater diversity of birds than do plant communities that are predominantly spruce. The greater number of species seems to be related to the structural complexity of available habitat - a feature particularly notable in alluvial areas. For instance, a single species may require one type of habitat for nesting, a second for territorial display, and a third for foraging. Most studies of birds separate habitats on the basis of plant community rather than origin of parent material, so there are no data to provide direct comparisons of alluvial and non-alluvial sites. Because alluvial ecosystems support several plant communities and often exhibit many ecotones, they probably host the greatest variety of terrestrial bird species.

Non-migratory game birds that use alluvial areas along rivers include grouse and ptarmigan. In southern parts of the Mackenzie River Basin, ruffed grouse are common in deciduous and mixed forests, often on alluvial terraces. In northern parts of the basin, willow ptarmigan are common. In winter, flocks of several hundred ptarmigan may move into appropriate semi-open habitat, often alluvial sites along aggrading banks. Their requirement seems to be willows with buds protruding above the snow for food, taller willow for shelter and soft snow for burrowing.

Northern deltas are most important to continental waterfowl populations in years when drought strikes the prairies. Then thousands of birds by-pass their intended prairie destinations and spend the summer on deltas within the Mackenzie River Basin. The northern deltas may also be of continuously increasing importance for waterfowl production because as prairie potholes disappear a greater proportion of the annual continental waterfowl production may be coming from the north.

The importance of alluvial areas to wildlife could be assessed more objectively if comparative data were available on primary and secondary productivity in alluvial and non-alluvial areas. The common assumption of high productivity on alluvial areas may or may not be warranted in comparison with sites that support similar species elsewhere. If there is, in fact, a high secondary productivity, in the form of herbivorous animal biomass, it may be a response to a relatively high primary productivity on alluvial sites. However, it may also be due to a relatively greater proportion of primary production, and therefore energy, being available as food to consumers because vegetation is in early succession stages.

Data to directly compare nutrient values of plant species used by wildlife on alluvial areas with nutrient values of plants used by wildlife on non-alluvial areas are generally unavailable. Existing data tend to relate to a single species rather than to communities of organisms and generally do not distinguish between alluvial and non-alluvial areas.

The reasons for choice of certain plant species as food by wildlife may be nutrient content, but a variety of other factors may also be involved, including: succulence or palatability; growth form; height of shrubs; season of use; water depth in relation to growth forms; or type and abundance of associated plants. Data which are available show no clear correlation between choice of food species by animals and nutrient value of plant taken. Nutrient requirements of northern animals are not known in detail. Specific data have been collected relating to single species at single sites, within and outside the Mackenzie River Basin. However, comparisons usually have to be made with nutrient requirements of domestic herbivores or other distantly related species.

Alluvial areas in the Mackenzie River Basin are important at some time of year to some populations of nearly all wildlife species of economic importance, with the possible exceptions of barren-ground and woodland caribou. Even marten, traditionally considered a species restricted to pure conifer stands, occur along upland river valleys and terraces in mixed forests where prey densities are high.

In summary, direct comparisons of wildlife that inhabit alluvial sites with the same species or species groups in non-alluvial locations do not appear to be possible. Reliable population density, mortality, and natality information is not available. Few non-alluvial sites in the Mackenzie River Basin support an assemblage of wildlife similar to that found in alluvial areas, but the glaciofluvial Brackett Lake wetland, which has been repeatedly disturbed by fire, is one such location. It supports muskrats, beaver, staging waterfowl, nesting ducks, and wintering moose, and illustrates the fact that concentrations of wildlife associated with alluvial ecosystems may also be found in non-alluvial locations where their habitat requirements are met. In the absence of more quantitative information, it must be concluded that whether an area is alluvial or non-alluvial in origin if it provides the necessary type and structure of plant communities and other physical habitat requirements for a species, that species will usually inhabit the area. Alluvial ecosystems stand out as areas of special importance to wildlife because they are areas of dynamic equilibrium and also because of their widespread distribution throughout the Mackenzie River Basin.

G. Conclusions

Comparisons of ecological processes outlined for alluvial sites in the Mackenzie River Basin with those described for floodplains and deltas elsewhere suggest that many of the principles are of widespread application to flood-prone ecosystems. Flooding and subsequent reductions of water levels appear to be the key external forces that determine vegetational composition and productivity on floodplains. However, flooding can either enhance or stress an alluvial ecosystem depending on the frequency, timing, and intensity. Over the annual cycle, benefits seem to exceed metabolic costs in natural floodplains where organisms are well adapted to the flooding regime. Extremes of stagnant water or abrasive flooding stress the biotic community and reduce productivity. In contrast, seasonal flooding of natural floodplains in natural watersheds generally increases productivity as compared with adjacent uplands. Thus, riparian productivity is reduced when normal seasonal flooding is eliminated or diminished by dams because subsidies are reduced and stresses increased (Odum 1979).

Evidence from a broad range of ecological studies indicates that with animal populations, both density and diversity of species tends to be higher at the land-water ecotone than in adjacent uplands. Not only are many small species restricted to alluvial habitats, but many large animals require access to stream or lake margins to survive even though they may spend much of their time elsewhere (Odum 1979). Whether the land-water ecotone is taken to mean the entire floodplain or only channel margins, there is evidence that flood-prone areas possess several characteristics that make them stand out as areas of special significance.

Superimposed upon the distinctive ecological processes within alluvial sites are certain specialized features of resident species. Some animals that inhabit alluvial ecosystems are particularly well adapted either to take advantage of opportunities offered by a rapidly changing environment or to avoid some negative consequences of it. Waterfowl are among the flexible species. Birds that would normally nest on the prairies can bypass them in years of drought and spend the summer on northern deltas. In many areas, renesting is possible if the first nest is destroyed, by early summer flooding, for example. Other examples of wildlife adaptations centre around reproductive potential once favourable conditions are created by flooding and by low water levels. Muskrats are prolific and can colonize newly created habitats soon after they become available. A single female will raise two or three litters each summer and populations have risen as much as 500% over a three-year period. Among ungulates, moose are particularly well able to respond to changes in quantity or quality of available habitat because of their relatively high reproductive potential. If range conditions are good, a high proportion of moose yearlings may breed and older females commonly produce twins.

A number of different hydrological processes control the formation and destruction of alluvial ecosystems but in the Mackenzie Basin flooding is the dominant force. Directly and indirectly, floods are responsible for a continued high primary production of plant material on alluvial sites and this, in turn, supports a relatively high secondary production by animals. In addition, the combination of plant and animal species that occur on alluvial sites is often distinctly different from that on nearby non-alluvial sites.

The major deltas of the Mackenzie River Basin - the Peace-Athabasca, Slave, and Mackenzie - are among the largest concentrations of wetlands in the basin. Their areal extent and their many lakes, in contrast to the essentially linear nature of river valley alluvial areas, provide habitats for vegetation and wildlife unlike those along the rivers.

Although alluvial sites make up a small percentage of the total area within the Mackenzie River Basin, studies of forest and agricultural potential within the basin have confirmed findings from elsewhere that alluvial sites are the most productive sites in any given region. Along several tributaries of the Mackenzie River, it is known that the regionally most productive sites, from a forestry point of view, are those that develop on recent alluvium or on river terraces.

The distinct plant and animal communities of alluvial sites, and their relatively high productivities, are the end result of a complex web of climatic, fluvial and biological processes that interact to form areas of special significance along river channels and on deltas of the Mackenzie River Basin. The processes involved in these intricate relationships are a result of depositional and erosional forces, vegetational responses to fluvial processes, vegetational controls over wildlife use of alluvial sites, and a variety of ecological and physiological adaptations that allow resident plant and animal species to effectively use the dynamic habitats of flood-prone areas.

Thus, providing annual floods continue, alluvial ecosystems represent essentially permanent disclimax communities of plants and animals, at least when viewed in terms of the human time span. Furthermore, the distribution of channel systems ensures that there are alluvial sites throughout the entire Mackenzie River Basin, with the result that plant and animal species from alluvial sites are available to colonize suitable non-alluvial locations nearby when disturbances, such as fire, make them available. Added to the special feature of alluvial sites, as outlined in previous sections, is the fact that non-deltaic alluvial sites are located in river valleys that possess additional features of special importance to plant and animal communities. The physiographic diversity and distinctive microclimates of valley slopes give river valleys other features of biological importance, in addition to the special characteristics that typify flood-prone parts of the valleys.

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APPENDIX 1

GLOSSARY OF TECHNICAL TERMS

Active layer - the layer of the soil that usually freezes in the winter and thaws in summer, found immediately above perennially frozen ground.

Adventitious root - a root that arises from any plant part other than the primary root or its branches; adventitious roots often develop on stems above the normal rooting zone.

Aggradation - filling in or leveling by deposition.

Albedo - that fraction of the total light falling on a surface which is reflected back.

Allogenic processes - forces (usually physical) that act from outside an ecosystem or community to create a change.

Alluvium (alluvial) - materials such as clay, silt, sand or gravel deposited by modern rivers and streams.

Autogenic processes - biotic processes within an ecosystem or community that cause the community to change.

Bankfull stage - the flow stage of a river in which the stream completely fills its channel so that the elevation of the water surface coincides with the bank margins.

Bogs - peat-covered areas with a high water table and a surface carpet of mosses, chiefly **Sphagnum**. The bog surface is virtually isolated from mineral soil waters; hence the surface bog waters and peat are strongly acid and upper peat layers are extremely deficient in mineral nutrients. Bogs may be treed or treeless and are frequently characterized by a layer of ericaceous shrubs.

Braided stream - a stream flowing in several channels that repeatedly divide and re-unite.

Catkin - an arrangement of flowers that resembles a scaly spike. The flowers are usually unisexual and lack petals.

Climax vegetation - the terminal vegetation type of a successional sequence. It is the most stable plant community of a series.

Convectional precipitation - precipitation that results from vertical transport and mixing of air masses.

Discharge - the flow rate of water expressed as volume per unit of time.

Disclimax - a particular type of vegetation that is maintained as a result of recurrent disturbances; the agent responsible for the disturbance prevents the establishment of a climatic climax community; repeated browsing or grazing is a common cause of disclimax stands of vegetation.

Dynamic equilibrium - a condition in which several processes act simultaneously to maintain a system in an overall state that does not change with time; dynamic equilibrium implies a balance of income and outgo, superimposed upon a continuous flow of matter and energy through a community.

Ecotone - a transition between two or more diverse plant communities.

Edaphic - pertaining to the soil; an edaphic community is one that results from or is influenced by factors inherent in the soil or other substrate (for example, drainage) rather than by climatic factors.

Emergent species - an aquatic plant that has its stems or leaves extending above the water surface (for example bulrush or cat-tail).

Ericaceous - members of the Ericaceae or heath family; often shrubby plants with leathery leaves, such as bearberry, heather, or Labrador tea.

Estuary - a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measureably diluted with fresh water.

Fens - peatlands characterized by surface layers of poorly to moderately decomposed peat. Sedges dominate in fens although grasses, reeds, shrubs, and a sparse layer of trees may be present. Usually there is slow internal drainage of waters which are less acidic than waters of bogs in the same area.

Floodplain - the land bordering a stream built up of sediments from overflow of the stream and subject to inundation when the stream is at flood stage.

Fluvial processes - processes involved in the sculpturing and redistribution of land areas as a result of weathering, mass-wasting and erosion caused by running water.

Frazil ice - a mush-like mixture of water and ice particles, formed by freezing in turbulent flowing water.

Geomorphic processes - all those physical and chemical changes that result in a modification of the earth's surficial form.

Glaciofluvial - pertaining to streams fed by melting glaciers, or to the deposits and landforms produced by streams of glacial origin.

Hydrology - the science that treats the occurrence, circulation, distribution and properties of the waters of the earth and their reaction with the environment.

Hydrograph - a graphic representation of the stage, flow, velocity, or other characteristics of water at a given point as a function of time.

Levee - low ridges that parallel a river course. Levees are highest near the river and slope gradually away from it; their greater height near the stream channel is due to the cumulative effect of sudden loss in transporting power when a river overspreads its banks.

Lipid - one of a class of compounds of hydrocarbons which include waxes and fats.

Microclimate - the climate near the ground, as influenced by variations in kind of soil, vegetation cover, shading or wind protection.

Mortality - death rate.

Muskeg - a term that refers to bogs or boggy areas, often having a sparse cover of black spruce trees.

Natality - birth rate.

Negative energy balance - an arithmetic balance of energy inputs and outputs whose sum is negative, with the result that there is a net loss or reduction of energy.

Orographic precipitation - precipitation that results from the lifting of moist air over a barrier such as a mountain range.

Oxbow - an abandoned channel of a former stream meander.

Perched basin - a basin whose surface water level is above that of the surrounding general water table and is separated from underlying groundwater by an impermeable bed.

Permafrost - perennially frozen ground, occurring wherever the temperature remains below 0°C for several years.

Point bar - a depositional feature on the convex bank of a meandering river channel; usually a series of discrete ridges due to the periodic accumulation of sediment.

Primary productivity - the rate at which radiant energy is stored by the photosynthetic activity of green plants in the form of organic substances which can be used as food materials.

Rhizome (rhizomatous) - a more or less elongated, usually underground, horizontal or ascending stem.

Secondary productivity - the rate of energy storage by consumer organisms (animals) in an ecosystem.

Sere - the whole sequence of communities that replace one another in a given area. The transitory communities that precede the climax vegetation are called seral stages.

Shoals - a submerged elevation rising from the bed of a body of water and sometimes exposed at low water.

Short-wave radiation - a term used to distinguish solar radiation in the visible and near-visible portions of the electromagnetic spectrum, as opposed to long wave radiation.

Siltation - deposition of silt suspended in a body of standing water.

Slip-off slope - long low gentle slope on the inside of the downstream face of a stream meander.

Slumping - a type of landslide characterized by the downward slipping of a mass of rock or unconsolidated material, moving as a unit or several subsidiary movements.

Solifluction - downslope soil movement or soil flow.

Staging site - location at which waterfowl or other migratory birds stop during spring and fall migrations to rest and feed; staging refers to the act of using a staging site.

Storm surge - a rise above normal water level on the open coast due only to the action of wind stress on the water surface.

Succession - an orderly process of changes in species structure and community processes with time in a biological community; succession is reasonably directional and therefore predictable.

Terrace - a nearly level, usually narrow plain bordering a river or lake; alluvial terraces are particularly prominent along valleys that carried glacial outwash.

Thermokarst - depressional erosional features formed in a permafrost region by melting ground ice; thermally created depressions that contain water are called thermokarst lakes.

Ungulate - hoofed animals such as moose, bison, deer or reindeer.

Understory - the lower of two vegetation layers on a site, such as shrubs beneath trees.

Vegetative propagation - plant reproduction not involving seeds (for example growth of new stems from buried branches or formation of suckers from roots).

Water table - the upper surface of the zone of water saturation in unconfined material.

APPENDIX 2

COMMON AND SCIENTIFIC NAMES OF PLANTS REFERRED TO IN TEXT.

(Scientific names are from: Moss E.H. 1959. Flora of Alberta. University of Toronto Press. 546 p; Porsild, A.E. and W.J. Cody. 1980. Vascular plants of continental Northwest Territories, Canada. National Museum of Natural Sciences, National Museums of Canada. 667 p.; Scoggan, H.J. 1978. The flora of Canada. Parts 1-4. National Museum of Natural Sciences. Publications in Botany No. 7 1711 pp.)

COMMON NAME	SCIENTIFIC NAME
Trees	
aspen	**Populus tremuloides**
birch	**Betula papyrifera**
poplar, balsam	**Populus balsamifera**
spruce, black	**Picea mariana**
spruce, white	**Picea glauca**
Shrubs	
alder	**Alnus**
alder, green	**Alnus crispa**
alder, grey	**Alnus incana**
bearberry	**Arctostaphylos**
birch, dwarf	**Betula glandulosa**
cranberry, mountain	**Vaccinium vitis-idaea**
dogwood, red-osier	**Cornus stolonifera**
rose	**Rosa**
soapberry	**Shepherdia canadensis**
tea, Labrador	**Ledum**
willow	**Salix**

willow, Alaska	Salix alaxensis
willow, sandbar	Salix interior

Graminoids

bentgrass, reed	Calamagrostis
bulrush	Scirpus
bulrush, common great	Scirpus validus
bur-reed	Sparganium
bur-reed, giant	Sparganium eurycarpum
cat-tail	Typha
cottongrass	Eriophorum
fescue	Festuca
foxtail	Alopecurus
horsetail	Equisetum
horsetail, marsh	Equisetum palustre
horsetail, meadow	Equisetum pratense
horsetail, water	Equisetum fluviatile
manna-grass	Glyceria
reed	Phragmites communis
rush	Juncus
rush, spike	Eleocharis
sedge	Carex
sedge, beaked	Carex rostrata
sedge, slough	Carex atherodes
sweetflag	Acorus
whitetop	Scolochloa festucacea

Herbs

buttercup	Ranunculus
bur-marigold	Bidens cernua
milfoil	Myriophyllum
pondweed	Potamogeton
ragwort, marsh	Senecio congestus
sarsaparilla	Aralia nudicaulis
vetch, sweet	Hedysarum
vetchling	Lathyrus ochroleucus

Mosses and Lichens

mosses, feather	Hylocomium, Pleurozium
lichen, reindeer	Cladonia
sphagnum	Sphagnum

APPENDIX 3

COMMON AND SCIENTIFIC NAMES OF MAMMALS REFERRED TO IN TEXT

(Scientific names are from: Banfield, A.W.F. 1974. The mammals of Canada. University of Toronto Press. 438 p.)

COMMON NAME	SCIENTIFIC NAME
bear, black	Ursus americanus
bear, grizzly	Ursus arctos
beaver	Castor canadensis
bison, plains	Bison bison bison
bison, wood	Bison bison athabascae
caribou, barren-ground	Rangifer tarandus groenlandicus
caribou, woodland	Rangifer tarandus caribou
coyote	Canis latrans
deer, mule	Odocoileus hemionus
elk	Cervus canadensis
fox, colored	Vulpes vulpes
hare, snowshoe	Lepus americanus
lynx	Lynx lynx
marten	Martes americana
mink	Mustela vison
moose	Alces alces
muskrat	Ondatra zibethicus
reindeer	Rangifer tarandus tarandus
wolf	Canis lupus
whale, white	Delphinapterus leucas

APPENDIX 4

COMMON AND SCIENTIFIC NAMES OF BIRDS REFERRED TO IN TEXT

(Scientific names are from: Godfrey, W.E. 1966. The birds of Canada. National Museums of Canada, Bulletin 203. 428 p.)

COMMON NAME	SCIENTIFIC NAME
brant, black	**Branta bernicla nigricans**
bufflehead	**Bucephala albeola**
crane, sandhill	**Grus canadensis**
ducks, dabbling	Subfamily **Anatinae**
ducks, diving	Subfamily **Aythyinae**
eagle, bald	**Haliaeetus leucocephalus**
falcon, peregrine	**Falco peregrinus**
flicker, common	**Colaptes auratus**
flycatcher, least	**Empidonax minimus**
geese	Subfamily **Anserinae**
geese, Canada	**Branta canadensis**
geese, lesser snow	**Chen caerulescens**
geese, white fronted	**Anser albifrons**
godwit, Hudsonian	**Limosa haemastica**
goldeneye, common	**Bucephala clangula**
grouse, ruffed	**Bonasa umbellus**
gull, California	**Larus californicus**
hawk, rough legged	**Buteo lagopus**
kestrel, American	**Falco sparverius**
merlin	**Falco columbarius**

ptarmigan, willow	**Lagopus lagopus**
redstart, American	**Setophaga ruticilla**
robin	**Turdus migratorius**
sandpiper, Bairds	**Erolia bairdii**
sandpiper, pectoral	**Erolia melanotos**
sandpiper, semipalmated	**Ereunetes pusillus**
sparrow, chipping	**Spizella passerina**
sparrow, clay-colored	**Spizella pallida**
swan, whistling	**Olor columbianus**
tern, Arctic	**Sterna paradisaea**
tern, black	**Chlidonias niger**
thrush, hermit	**Hylocichla guttata**
thrush, Swainsons	**Hylocichla ustulata**
vireo, red-eyed	**Vireo olivaceus**
warbler, black-throated green	**Dendroica virens**
warbler, magnolia	**Dendroica magnolia**
warbler, yellow	**Dendroica petechia**